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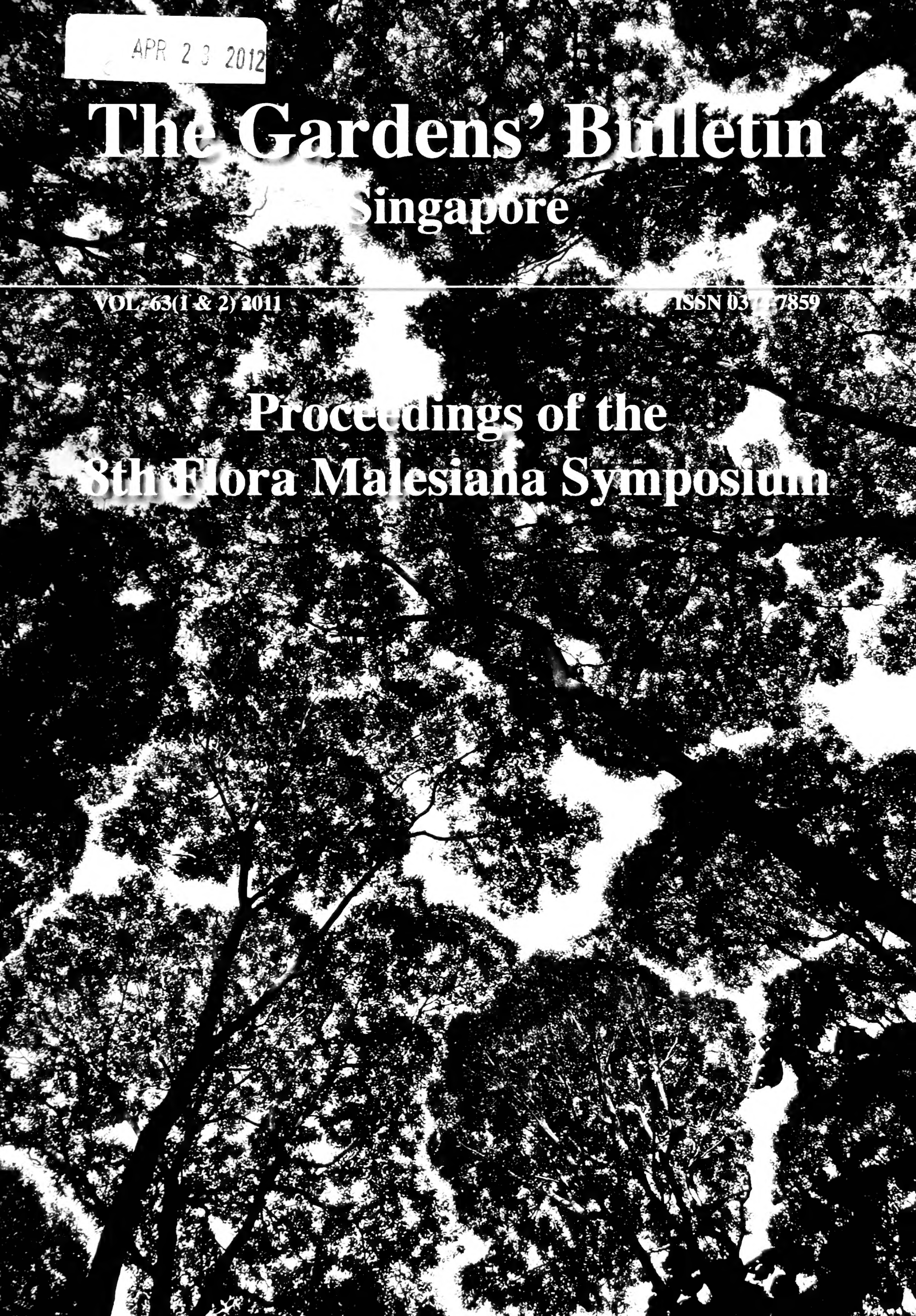

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(*continued on inside back cover*)

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ETHNOBOTANY

Georgius Everhardus Rumphius (1627–1702), the blind seer of Ambon

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ABSTRACT. Georg Eberhard Rumpf, better known as Rumphius (1627–1702) was a *Homo universalis* and is the undisputed patriarch of Malesian botany, zoology, geology (including fossils!), colonial history; pharmaceutical, architectural, juridical (local and Western), ethnological, linguistic, historical, and religious matters, including astrology and magic. To botanists he is best known for his *Herbarium amboinense* (1741–1750), the first account and sometimes the only one of Malesian plants. This is a 7-volume folio work with extensive descriptions and discussions in Latin and Dutch of about 1200 species with 811 full-page illustrations. A brief account of his life and works is given.

Keywords. Ambon, Dutch United East Indian Company, Herbarium amboinense, Malesia, natural science, Rumpf, Rumphius, VOC

Introduction

Many articles and books have been written about Georg Eberhard Rumpf (Georgius Everhardus Rumphius in Latin), better known as Rumphius (1627–1702) and his observations in the Moluccas (Fig. 1, 2), which have given him an everlasting place of honour in the history of natural science (see Appendix A for a selection). Only a few of these publications were in English, the last one by Beekman (1999), who translated *d'Amboinschen Rariteitkamer* (1705), the Amboinese Curiosity Cabinet. This deals mainly with animals, mineralogy, and geology, explicitly recognising zoological fossils. European scientists regarded these as remnants from before the Deluge, or were created by the Devil to confuse good Christians. Some modern Creationists still think so. Every taxonomist in Malesia has encountered species named after him: "*rumphii*", "*rumphianus*", or based on taxa first described in his works.

Rumphius and Ambon

Ambon island (Pulau Ambon) in the 17th century (Fig. 3) was the centre of the spice trade: cloves, nutmeg, mace, and pepper. These commodities were very much in demand in Europe and worth a fortune once there. At one time for a bag of pepper one could buy an imposing house in a major town in The Netherlands! The organisation

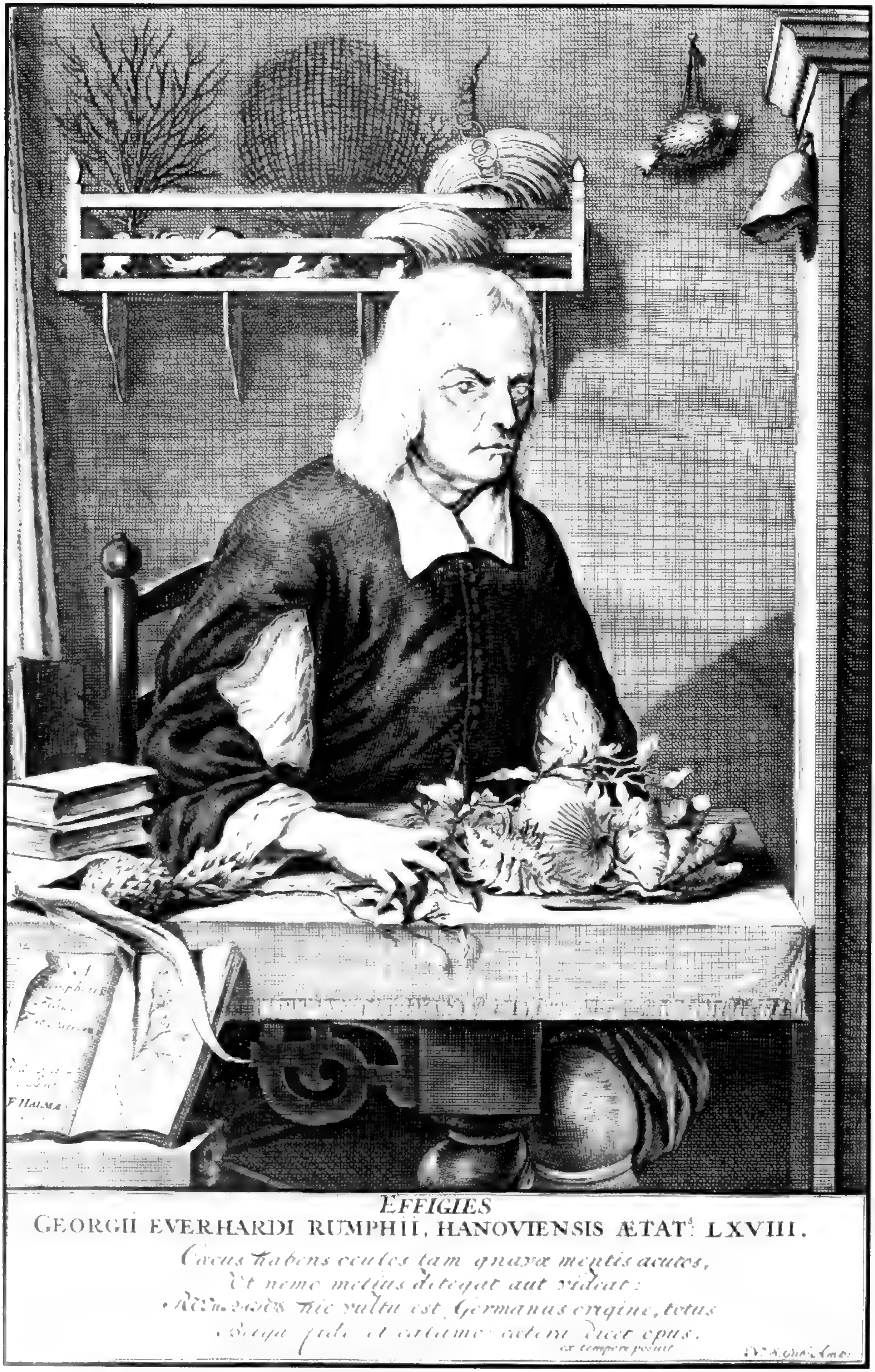

Fig. 1. Portrait of Rumphius at age 68 by his son Paulus.

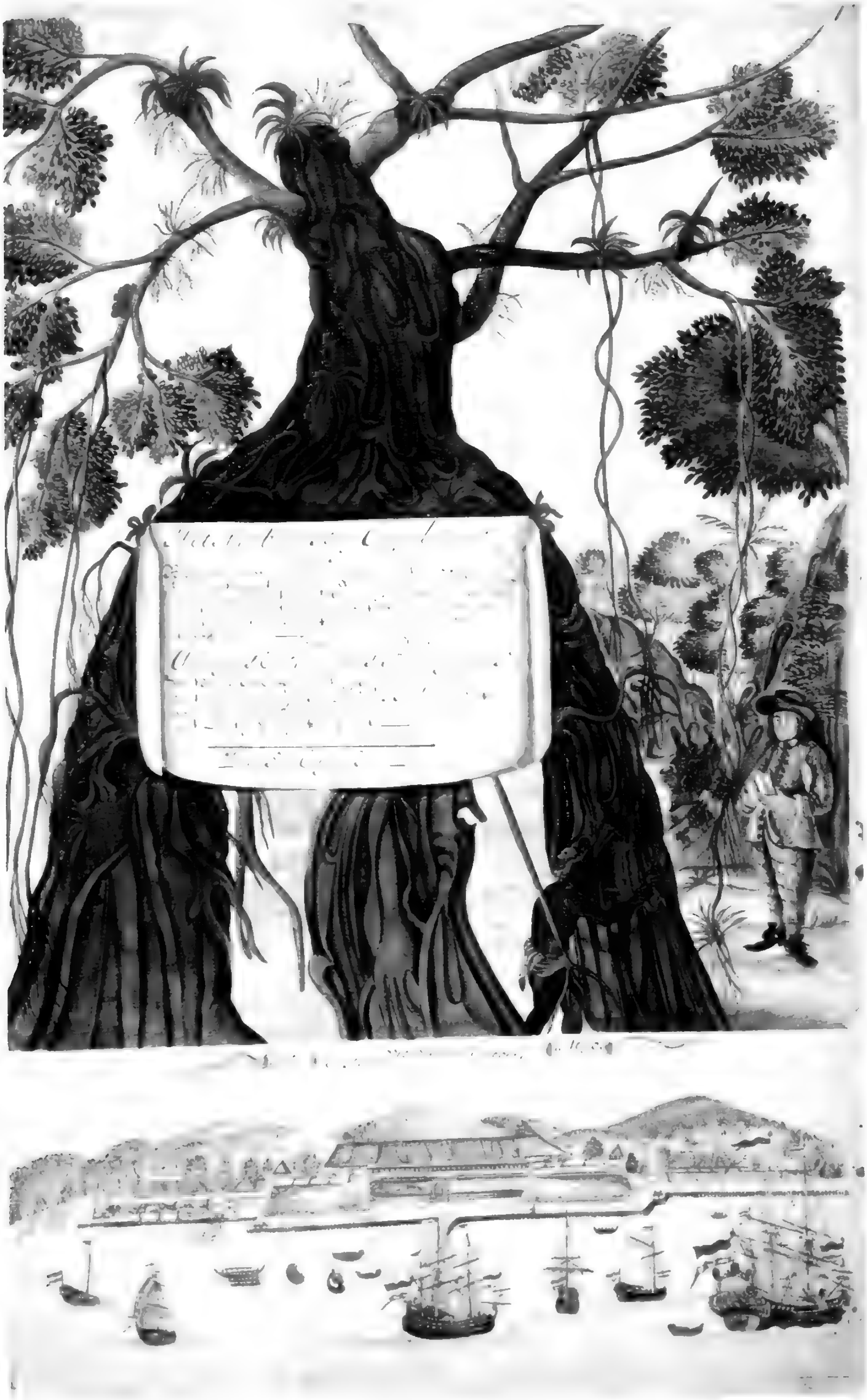

Fig. 2. The title page of the Auctuarium manuscript in the University Library of Leiden depicts a man, who might well be Rumphius, making notes under a remarkable fig. Below: roads of Ambon in 1690.

that ran the business was the Dutch *Vereenigde Oost Indische Compagnie* (VOC) (the United East Indian Company), a state within a state with its own navy, army, fortresses, trading posts, and diplomatic treatises with local leaders and political fractions. Its settlements were the predecessors of the Dutch East Indies, but also of the Republic of Ghana, and of South Africa, with settlements in many places, of note in the Arabian coast, S India, Sri Lanka (think of cinnamon!), Malaysia, Japan, and through Taiwan with China (think of the introduction of China ware, silk and tea in Europe!).

It is a sad thing that the identity of *Rumphia amboinensis* L. is unknown. Linnaeus based this on a plate in Rheede's *Hortus malabaricus* for a species from South India, a place where Rumphius had never been and whatever the identity of the species, it surely is not Amboinese. It just shows how little Linnaeus knew about geography, sometimes his provenance "India" even refers to the West Indies...

Other generic eponyms in zoology are the gorgonian *Rumphella* Bayer (1955), called "sea tree" by Rumphius, because at that time everything that moved was an animal, and what didn't was a plant. Linnaeus, also, regarded sponges (*Spongia* L.) as algae... There are also the sea urchins *Rumphia* Desor (1846; Miocene to Recent of the Indo-Pacific), *Neorumphia* Durham (1954), and *Rumphiocrinus* Wanner (1924). However, the butterfly *Rumphia* Pagenstecher (1909) is a typographical error for

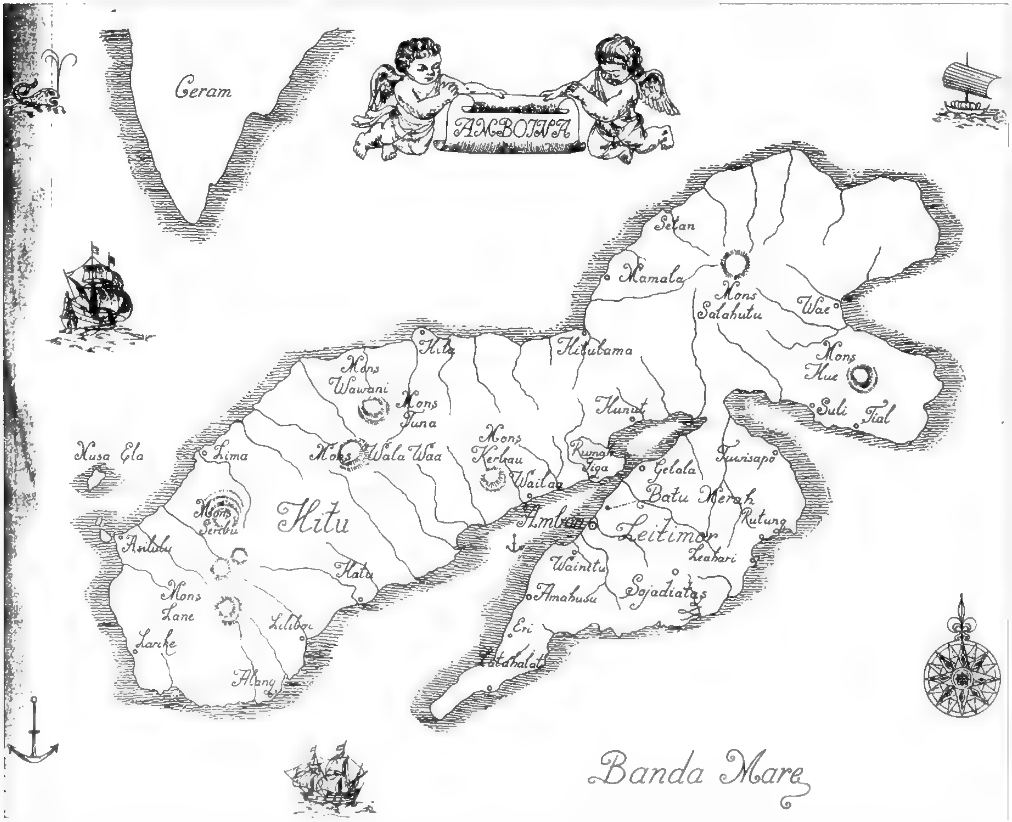

Fig. 3. Ambon.

Ramphia Guinée (1852). The botanical journal Rumphia appeared between 1836 and 1849. There is even a Rumphius Range in the Lorentz Park in Indonesian New Guinea.

Rumphius was born in at the end of 1627 in Wolfersheim, Hessen, Germany. His mother came from Cleve (Kleef) near the Dutch border, where at the time Dutch was spoken, which would explain his impeccable and even innovative command of that language. His father was an engineer, a builder of fortresses, and passed on this knowledge to his son. Georg had a good education and finished the Gymnasium, but did not go the University and did not get a degree in Medicine in nearby Hanau as was later suggested.

As he said later he wanted to see something of the world and in 1646 enrolled as a soldier, thinking that he would go the East Mediterranean, but instead he headed for Barbice in the Guyanas where the West Indian Company (WIC) was involved in wars with the Portuguese and Indians. There is still a saying in The Netherlands: "going to the barbiesjes", that is, to meet certain death. Fortunately for him (and us) he somehow landed up in Portugal, where he served as a mercenary soldier for three years after which he was dismissed, possibly because the Catholics there didn't trust Protestants like him. He returned to Germany for two years.

He may well have heard about the riches of the East Indies from his Dutch relatives and wished to see them for himself. And thus at Christmas 1652 he left from The Netherlands as an *adelborst* (midshipman) with the VOC. Note that he would have had a much higher rank if he had had an academic education and, especially, when he had been a physician. These were very much sought after by the VOC in view of the high rate of injuries, diseases and deaths that plagued the fleets and garrisons. Later authors thought he was a medical doctor, but he denied this and in fact he was an amateur naturalist and a self-made man in the best sense of the word.

By the end of 1653 he arrived in Pulau Ambon, never to leave the Moluccas again. His father's education now proved fruitful in the planning and construction of fortifications. However, soon after 1657, he switched from the military to the civilian and was appointed as Junior Merchant (*onderkoopman*) at Larike, on the West coast of Hitu. There he married Susanna, a local woman, possibly Chinese, according to European marriage records. He named the orchid *Flos susannae* after her, now *Pecteilis susannae* (L.) Raf. "in memory of her who during her life was my first companion and assistant in the finding of herbs and plants, she was the first to show me this flower" (Fig. 4).

Larike was a back-water dump and because he had so little to do he could devote a great deal of his time in the studies of the Treasuries of Nature. Rumphius sent specimens to Europe which are not recorded in the VOC archives. This is not so strange, as the VOC did its utmost to prevent exports and forbid private mailings. Of course, everybody circumvented these rules. Rumphius is commended by all for his honesty, but apparently he had his channels. You might say that he was less corrupt than the others...

In 1701 he also smuggled out the manuscript of *d'Amboinsche Rariteitkamer* (Fig. 5) to the mayor of Delft, Hendrik d'Acquet. It is interesting to note that some drawings of shells were made by Maria Sybille Merian (1647–1717), who also hand

Fig. 4. Flos susannae, *Pecteilis susannae* (L.) Raf. (Orchidaceae).

coloured a few now priceless copies (Fig. 6). Where Rumphius was the founder of zoology and botany in the Moluccas, she was that for Surinam.

He was elected as a member of what is now the oldest science society in the world, the *Academia naturae curiosorum* of the German Roman Empire (founded in 1657, today still in existence as the Leopoldina). Members were given nicknames, his was "Plinius", a most honorific title as it was after the Roman procurator ('administrator') Gaius Plinius Secundus (23–79 A.D.), killed in the eruption of the Vesuvius which buried Pompeii and Herculaneum, and who was one of the founders of European natural sciences. His influence lasted for 1500 years until the end of the Middle Ages. Actually, Rumphius was more than Plinius, as the latter compiled existing knowledge, while Rumphius did mention his sources, but added personal experience. Blume, the second Director of the Kebun Raya Bogor, and then the first Director of the Rijksherbarium, in his turn as a member, was called "Rumphius", but although a Medical Doctor from the Leiden University, he was a scientist of an entirely different kind.

Thirteen of Rumphius's letters were published in the Society's journal *Miscellanea Curiosa*. In 1682 he sent shells, sea animals, minerals, resins, fossils, and some parts of plants in a cabinet made from 56 different kinds of wood to the Grand-duke of Toscane, Cosimo III de'Medici (1639–1723). Unfortunately, the chest and its contents have been lost, as the original labels have probably been replaced. Some shells may be present in the State Museum in Vienna, and perhaps some fragments of palms in Florence.

In 1660 he was promoted to Merchant (*koopman*) and moved to Hila, a much more civilised place, where he lived like a prince: daily fresh venison, plenty of fish, and sheep, geese, ducks, and chickens, horses with superb bridles, some of pure silver. He had a one-gun vessel with 40 rowers. His gardens yielded cabbages, endives, lettuce, parsley, Chinese radishes, etc. He even had a small zoo. Life was pretty good!

In 1662 he became Senior Merchant (*opperkoopman*). He then earned the extra-ordinary salary of 24 rixdollars (60 guilders, or 1200 Dutch shillings) a month. In comparison, Jan van Riebeeck, the famous Governor of the Cape, got "only" 21. He stayed there for 10 years, rather exceptional, as VOC employees usually were translocated after about 5 years to prevent too good connections for graft and smuggling. This may well be due to the good opinion his superiors had of his honesty.

In August 1663, he wrote a letter to the Board of the VOC in which he asked for permission to have books sent for his work on the plants and animals of the East Indies. This was granted, but only in 1666 did he receive them. One of his arguments was, that God in His wisdom had provided local herbs to cure local diseases, so a better knowledge of what was available would be beneficial to all. The medicines shipped from The Netherlands were ineffective and often spoiled. He noted that although many local recipes might be fables, superstitions, or old wives' tales, they should be included as there might be some truth in them. Of course he lacked the occasion and time to try all medicines, but some he had "tested in mine own house, and with other families".

His accounts are not bone dry enumerations as was usual for herbals at the time, but every species got an extensive description, where it occurred, what it was used for, a recipe, anecdotes, and sometimes a joke. For instance, that newcomers (*orang baru*) were fooled with the resin of the pine *Agathis*, which they were told were lumps of sugar, with which they then went into hiding to quietly and privately enjoy the supposed delicacy. Of course he speaks much of diseases, health, birth, death, and

D'AMBOINSCHE
RARITEITKAMER,
Behelzende eene BESCHRYVINGE van allerhande
zoo weeke als harde
SCHAALVISSCHEN,
te weeten raare
KRABBEN, KREEFTEN,
en diergelyke Zeedieren,
als mede allerhande
HOORNTJES en SCHULPEN,
die men in d'Amboinſche Zee vindt:
Daar beneven zommige
MINERAALEN, GESTEENTEN,
en ſoorten van AARDE, die in d'Amboinſche, en zommige
omleggende Eilanden gevonden worden.
Verdeelt in drie Boeken,
En met nodige PRINTVERBEELDINGEN, alle naar 't leven getekent, voorzien.
Beſchreven door
GEORGIUS EVERHARDUS RUMPHIUS,
van Hanauw, Koopman en Raad in Amboina, mitsgaders Lid in d' *Academiæ Curioſorum Naturæ*,
in 't Duitſche Roomſche Ryk opgerecht, onder den naam van
PLINIUS INDICUS.

T'AMSTERDAM,
Gedrukt by FRANÇOIS HALMA, Boekverkoper
in Konſtantijn den Grooten.
1705.

Fig. 5. Title page of the Rariteitkamer.

all rituals concerned with these. A lot about sex, for that is part of life, but in a quiet, unsensational way, sometimes with a chuckle on human foolishness.

In 1666, he was temporarily appointed as *Secunde* ("second man"), a rank immediately under that of Governor, but was not confirmed in it. In compensation he was allowed to buy a piece of land. Here he created a Physic Garden, the first western type of botanical garden in Asia. He also had a forest garden long known as *Dusun Rumphius*. His contract with the VOC after having served 16 years, expired in 1668 and he was supposed to retire (at 41!) and go back to Europe. He was quite happy where he was and with what he was doing, so somehow he managed to extend his stay with retention of his salary forever. Life was good!

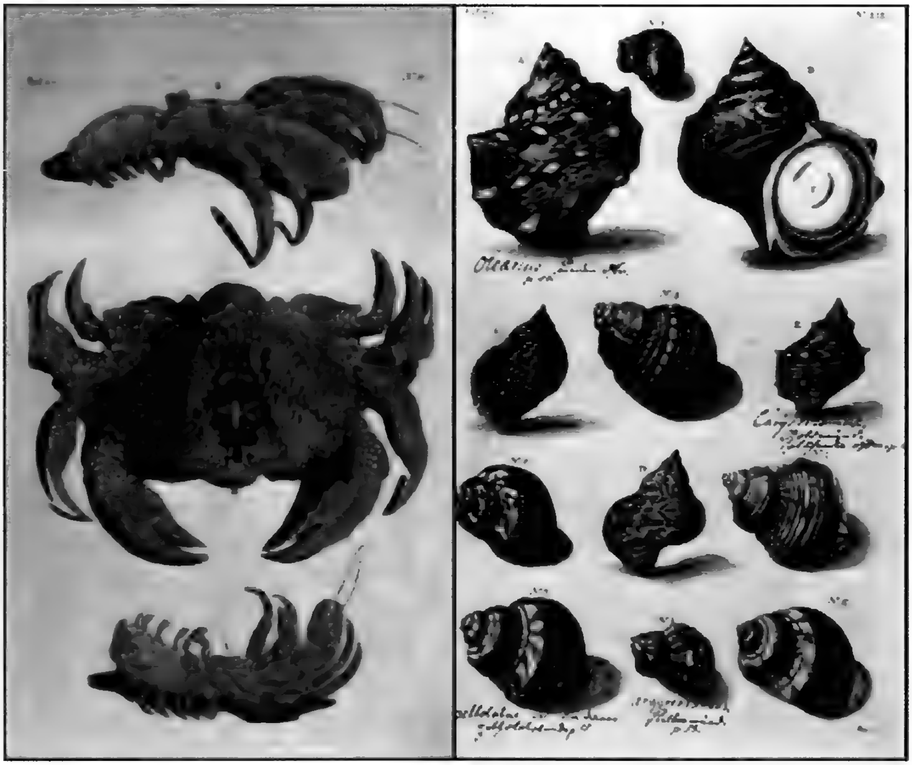

Fig. 6. A rare coloured plate of the Rariteitskabinet by Maria Sybille Merian.

Blindness and personal tragedy

Things changed considerably when in April 1670, at 42, he turned incurably blind (*glaucoma simplex*), about the worst thing that can happen to a dedicated naturalist. With the aid of his son and some assistants provided by the VOC, he continued with his work. The original manuscripts were in Latin, but because his assistants didn't know that language, he had to dictate them in Dutch. Here he showed his linguistic proficiency. Descriptive botany is a language by itself and in his time it had hardly evolved, certainly not in Dutch. Consulting literature will have been a problem, as these were of course in Latin and mainly dealt with the European flora. Works on Asian plants were by the Portuguese Garcia de Orta (1501–1568) published by Carolus Clusius (1567, 1582, 1593, 1605) from Goa in India, Hendrik Adriaan Rheede van Drakenstein's (1633–1691) 12-volume *Hortus malabaricus* (1678–1692) on South Indian ones, and a medical textbook by Jacob Bontius (1592–1631) for plants in Batavia. Later, Burman very carefully translated it all back again into Latin.

On Saturday, 17 February 1674, it was near the end of the Chinese New Year celebrations. Rumphius didn't attend, because, as he said, he couldn't see anything. Suddenly, there was a huge earthquake followed by tsunamis, killing 2322 people. A falling wall killed Susanna, two of their daughters, and a maid.

On Saturday, 11 January 1687, in Kota Ambon, where he now lived, he had another disaster. The town was razed by fire which destroyed his precious library, collections, and most of his manuscripts. Only parts of the *Herbarium amboinense* and about half of its plates were saved. Yet, undaunted by blindness and his awful losses, Rumphius dictated the lost chapters to his assistants again from memory and they managed to redraw the lost plates, probably under the supervision of his son Paulus.

By the end of 1690 the first part of his *magnum opus*, six books of the *Herbarium amboinense* were sent to Batavia, where they were copied for safe keeping. Not without reason, for it was a long and hazardous journey back to Europe. Indeed, the *Waterman* that carried them in 1692 was sunk by the French. A second copy was made including three additional books that had arrived in the meantime, and by August 1697 everything was safely in the Netherlands. A year later, the final three books were received. Two additional appendices were shipped by 1704.

On May 19, 1702, the Governor of Ambon wrote to the High Government at Batavia about Rumphius "nothing more was to be expected of that old gentleman, having lived his years", and on June 15 he died, 75 years old, very old for a European in the tropics. No special mention is made in the missives from Ambon, but casually, under another heading it is noted that he left 4000 rixdollars (10,000 guilders, or 200,000 Dutch shillings), quite a fortune, about two million Euro at present rates, and various pieces of estate (land, houses), the savings of about 50 years of duty.

Subsequent events

If you think the VOC would have been quick to publish this *magnum opus*, you are very much mistaken. Such a publication would be very expensive and would not provide any profits, so the Board would allow it as long as it would not cost the Company a penny. But there were no takers. Thus the manuscripts were locked up in their vaults.

Johannes Burman (1707–1779) was allowed by the VOC to prepare the manuscripts for publication in 1735. He meticulously translated Rumphius's poetic and flowery Dutch back into Latin and had etchings made of the drawings and colour plates. Take, for instance, the comparison Rumphius made of the wine-producing palm *Arenga pinnata* Merr.: "and thus it resembles in its ugly and uncouth habit a drunken

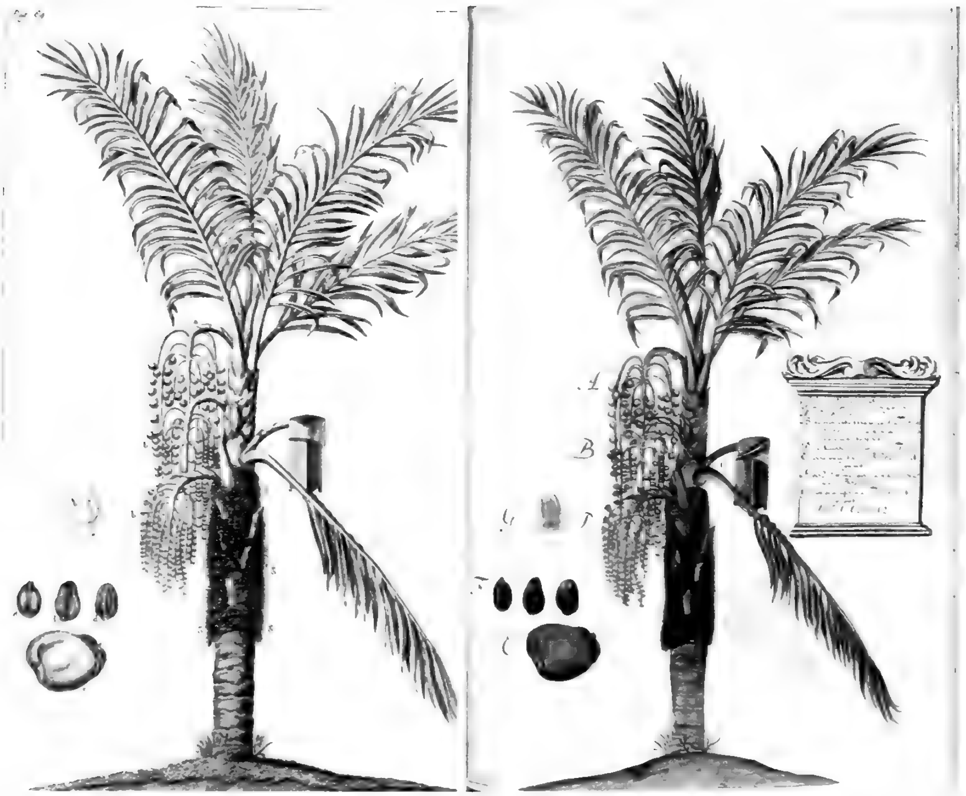

Fig. 7. *Arenga pinnata* Merr. as in the Herbarium amboinense (left) and in the manuscript of the Leiden University (right).

farmer as he jumps up from his sleep with mended rags and tussled hair. Indeed, this is the most ugly of all trees" (Fig. 7).

It was a very expensive publication, only 500 copies were printed, the set costing about 100 guilders (2000 Dutch shillings, now Euro 20,000), about a third of the income of a physician in Amsterdam. The original drawings often are in colour, but the books were already so expensive, that printing with coloured plates would make them completely out of reach. Thus it may happen that when Rumphius speaks of several species it is not quite clear which one has been depicted. An example is *Corona ariadnes punicea* with red flowers and *Corona ariadnes lutea* with yellow ones, but the legend does not state with one is represented. The coloured plate in the Leiden University Library shows the flowers to be red, so after more than 260 years we now know that the plate represents the *punicea* form, a synonym of *Hoya coronaria* Blume (Fig. 8). Similar problems may well be solved so easily.

Also, there have been only few attempts to recollect representative material. Most were only half-heartedly done, or the scientists died before arriving at the island. The most serious attempt was by Charles Budd Robinson (1871–1913), an American botanist sent there by Merrill, who made a large collection of Rumphian and non-

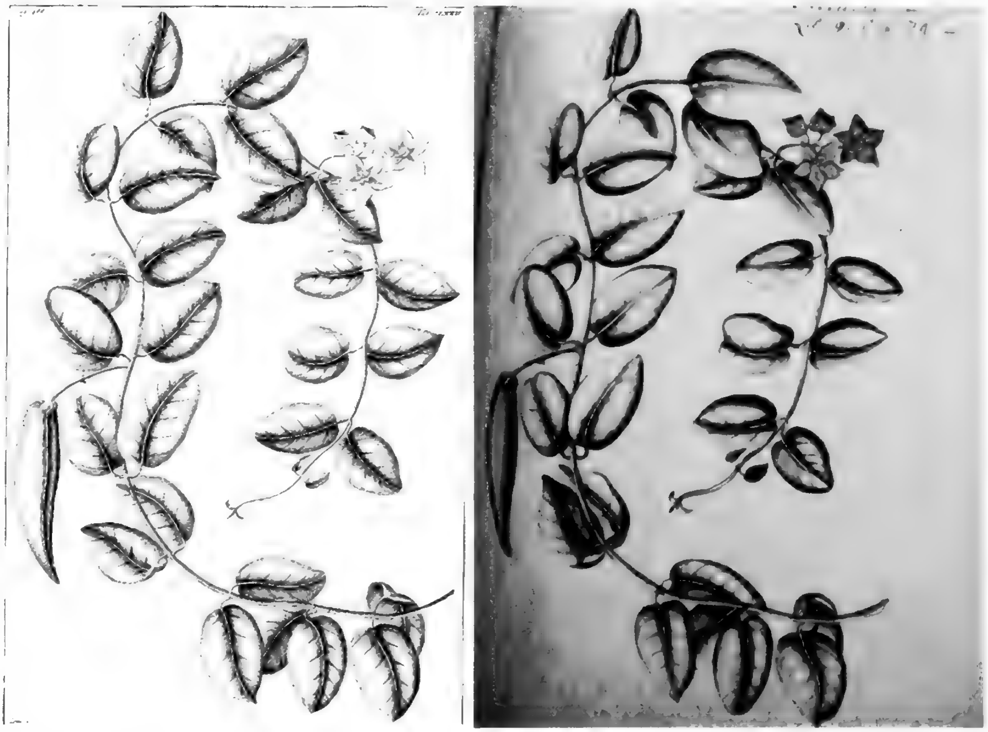

Fig. 8. *Hoya coronaria* Blume (Asclepiadaceae) as in the Herbarium amboinense (left) and in the manuscript of the Leiden University (right).

Rumphian species, but was prematurely murdered. Merrill distributed 18 duplicate series and by these many Rumphian taxa can be identified and the names exclusively based on them, neo- or epitypified (when the type is the illustration). The series have been deposited in A, BM, BO, F, K, L MO, NSW, NY, US. The top set with the original labels are in US, so in typifications these should be designated as the holotypes.

Anyway, these texts after so many years are still the only extensive source on the flora of Ambon. It is therefore remarkable that although there are various concordances, there has never been a reprint. Fortunately, the original texts can now be found on the internet, but unfortunately, very few have sufficient knowledge of Dutch and Latin to be able to read them. The good news now is that Monty Beekman (1939–2008) just before his death was able to finalise a translation into English which was released to the public on 20 June 2011, but was on 4 and 5 February 2011 officially presented to his widow, Faith Foss, by the Yale University Press at the Fairchild Botanic Gardens in Florida. This will make this seminal publication available to the Anglophone public and thus it will be a very valuable addition to the knowledge of the past, present, and future events of the Flora Malesiana. Of course the work has been extensively data mined. You will find references in Heyne's *Useful Plants of the Dutch East Indies*, sometimes as the only reference. From there they found their way to Burkill's *Dictionary of the Economic Products of the Malay Peninsula* and, more recently, into the publications of PROSEA.

Epitaph

Monuments have been raised for Rumphius, the first destroyed by tomb-robbers, the second (erected in 1824) hit by an Allied bomb in 1944, and a third was built in a slightly different place (yard of the Xaverius Junior High School, Jl. Pattimura) in 1996 (Buijze 2001: 282, fig.). I was in Ambon in April 2011 and visited this monument (Fig. 9). His house, however, was burned early 20th century. But no human activity can destroy the true monuments reminding us of this remarkable man: the works on plants, animals, and stones that he has left us.

Fig. 9. The Rumphius monument in the yard of the Xaverius Junior High School, Kota Ambon.

A *Homo universalis*: modest, unprepossessing, lenient to other people's views, an unbelievable resilience to disasters (blindness, loss of family, life work), perseverance under stress, yet with a persistent sense of humour—where this might easily and understandably have led to bitterness—with a continuous perspective curiosity, a perpetual surprise. We would do well to make him our example.

ACKNOWLEDGEMENTS. Special thanks are due to Dr. A. van de Beek (Amsterdam), Dr. P.D. Bostock (BRI), Mr. W. Buijze (The Hague), Ms. J. de Roode, Mssrs J. Cramer, J. Frankhuizen, and R.B.P Rijkschroeff of the University Library, Leiden, Dr. J. Dransfield (K), Dr. C.E. Jarvis and Dr. N.K.B. Robson (BM), Dr. D. Mabberley (L), Ms. K. Pocock of Yale University Press, London, Mr. O.P. van Zandwijk, Leiden, and Dr. G. Zijlstra (U) for various bits of information and technical help.

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Revision of the rattan genus *Daemonorops* (Palmae: Calamoideae) in Sulawesi using a phenetic analysis approach

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ABSTRACT. A phenetic analysis based on 27 morphometric characters of seven species of *Daemonorops* in Sulawesi recovered two groups with a similarity coefficient value of 0.51. Group A consists of *D. takanensis* and *D. lamprolepis* with a similarity coefficient value of 0.58. Group B is divided into subgroup B1 and subgroup B2, with a similarity coefficient value of 0.59. Group B1 consists of *D. macroptera, D. mogeana* and *D. robusta*. Group B2 consists of *D. riedeliana* and *D. sarasinorum*. An identification key to species and their descriptions are presented.

Keywords. Calamoideae, *Daemonorops*, Palmae, phonetic analysis, rattans, Sulawesi

Introduction

The palm flora of Sulawesi is distinctive and combines elements in common with Sunda, Sahul, the Philippines, and the Papua New Guinea. In the case of *Daemonorops*, all seven species recognised are endemic to the island and their affinities are not yet clear – whether with Sunda, Philippines or East Malesia. The genus *Daemonorops* itself is not well collected and poorly represented further east. Until recently, five species of *Daemonorops* were recorded for Sulawesi. As a result of recent fieldwork, a further two species have been recognised and described (Rustiami 2009). The purpose of this study to investigate morphological variation within *Daemonorops* in Sulawesi using a phenetic analysis of morphological data taken from herbarium specimens. This is done as a precursor to a treatment of the genus for Flora Malesiana.

The genus *Daemonorops* was described by Blume (1830), based on a single species which he named *Daemonorops melanochaetes* Blume. *Daemonorops* with more than 120 species is the second largest rattan genus after *Calamus*. It belongs to the subtribe *Calaminae*, tribe *Calameae* of the palm subfamily *Calamoideae*. Beccari (1911) divided *Daemonorops* into two sections based on the structure of the inflorescence, i.e., section *Cymbospatha* and section *Piptospatha*. Basically, the former have concave boat-shaped bracts which are at anthesis completely enclosed by the prophyll (the first bract) and splitting longitudinally to expose the flowers. In contrast, the bracts of the species in the latter section split to the base and only the lower part is enclosed by the prophyll. Of the 84 species identified, Beccari placed 32 species in the former section and 52 species in the latter. According to Furtado (1953) the bracts of section *Piptospatha* usually fall at anthesis and occasionally only the prophyll remains.

The name *Daemonorops* is derived from the Greek language combining two words *daemon* (devil) and *rops* (bush or shrub). This name reflects the fearsome appearance of the plant with its very robust leaf sheaths densely armed with long, blackish brown or cream-coloured spines (Dransfield et al. 2008).

Material and methods

Field work was carried out in several areas of Sulawesi to collect herbarium material. Herbarium specimen preparation followed the standard procedure of Dransfield (1986). Data or information recorded from the field include location; general habitat; altitude; association with other plant; vernacular name(s); uses; habit (solitary vs. clustered); stem attributes (height, diameter with/without leaf sheath, internode length, colour); characteristics of the leaves (length, leaflet arrangement, number of leaflets, length and width of leaflets); inflorescence characteristics (length, number of rachilla, colour); flower attributes (colour, scented/not scented); and fruit and seed characteristics (length and width, colour).

Field work data was combined with herbarium data for each taxon to obtain a more comprehensive set of morphological data. Morphological studies were carried out with specimens in several herbaria: Herbarium Bogoriense (BO), the Kew Herbarium (K) and the Leiden Herbarium (L).

A total of 300 herbarium specimens were studied following Vogel (1987) and Rifai (1976), using comparative morphological data as the main source of evidence in developing the species concept (Dransfield 1999).

Twenty seven morphometric characters were chosen (Table 1). These were scored using two simple states (absent – 0: present – 1). The data processing was carried out using the NT-Sys program 2.1 (Rohlf 1997). The descriptions of each species and identification key for *Daemonorops* were constructed based on the characters and character-states recorded.

Results and discussion

Fig. 1 shows the result of the phenetic analysis, in which seven species of *Daemonorops* are differentiated morphologically based on twenty seven characters. The specimens are clearly divisible into two groups (A and B) with a coefficient similarity value of 0.51. This value means that these two groups only have morphological similarity of around 51%. Group A consists of *D. takanensis* and *D. lamprolepis* where these two

Table 1. Morphometric characters used in the analysis.

1	Leaf sheath indumentum
2	Leaf sheath surface scales
3	Leaf sheath armed with short easily removed spines
4	Leaf sheath armed with brittle unequal, solitary spines
5	Leaf sheath armed with hair like spines
6	Leaf sheath armed with long, strongly attached spines
7	Leaf sheath armed with large, irregularly seriate spines
8	Ocrea present
9	Leaf sheath armed with short, scattered, seriate spines
10	Direction of spines on leaf sheath horizontal
11	Direction of spines pointing upward
12	Knee armature present
13	Leaf sheath mouth spiny
14	Petiole with indumentum
15	Leaflets arranged regularly
16	Leaflets arranged subdistantly
17	Leaflets arranged distantly
18	Transverse veinlets present
19	Corolla same size as the calyx
20	Corolla longer than the calyx
21	Fruit spherical
22	Fruit subglobose
23	Fruit ellipsoid
24	Seed surface smooth
25	Seed surface reticulate
26	Endosperm slightly ruminate
27	Endosperm deeply ruminate

species have a coefficient similarity value of 0.58. Group B divided into two subgroups, B1 and B2, with a coefficient similarity value of 0.59. From the phenogram we can see that *D. macroptera* and *D. mogeana* have a morphological similarity of around 81%. Those two species are close to *D. robusta*, with 67.4% similarity. In the other group we can see that *D. riedeliana* and *D. sarasinorum* have a similarity of around 77.4%.

Daemonorops mogeana, *D. macroptera* and *D. robusta* clustered in one group. This is because they have some similarities in their leaf sheath armature and leaflet arrangement. However they do differ in their general morphological appearance.

The stem of *Daemonorops* is covered by tightly sheathing, densely spiny, leaf sheaths. The diameter of the stem with the leaf sheaths can vary from a few mm to over 10 cm. Leaves consist of a tubular sheathing base, the leaf sheath, which arises from the node on the stem; at its upper end, the sheath narrows into the petiole that continues into the rachis or leaflet-bearing portion of the leaf. Although a petiole is usually present, it is sometimes very short or absent. In many species, the rachis is extended beyond the terminal leaflets into a barbed whip (cirrus) which acts as a

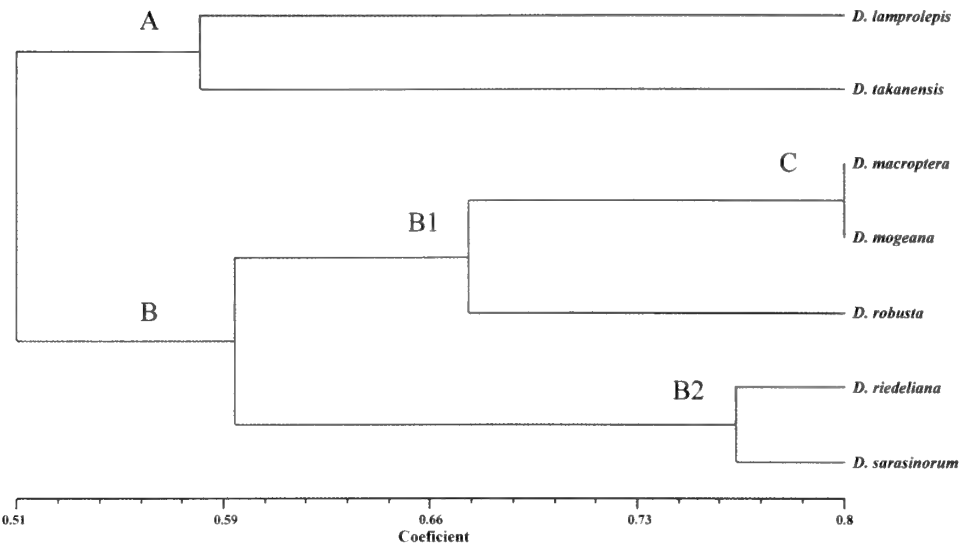

Fig. 1. Phenogram of morphological similarity among *Daemonorops* spp. from Sulawesi.

climbing organ (Dransfield & Manokaran 1994). Spine arrangement on the leaf sheath is remarkably diverse and frequently of diagnostic importance. Just below the petiole or leaf rachis, there is a marked swelling known as the knee. This character is also of some diagnostic importance, because some of the *Daemonorops* species do not have very obvious knees or the knee is only slightly developed.

As with most rattans, *Daemonorops* are dioecious, that is, female and male flowers are borne on different plants. The main axis bears a basal bract or prophyll, which may be short and tubular, or large. Branches are borne in the axils of subsequent bracts. The branches in turn bear bracts, the lowermost of which is usually empty, subsequent bracts subtending branches, and so on. The ultimate flower-bearing branches are termed partial inflorescences. On each female flower, there is a bracteole which immediately surrounding the flower, known as an involucre and an outer bract known as the involucrophore. Flowers are borne in dyads with two bracteoles in the female and in the male flowers are solitary with one bracteole.

Taxonomic treatment

Daemonorops Blume in J.A. & J.H. Schultes, Syst. Veg. 7(2): 1333 (1830).

Solitary or clustering rattans, acaulescent to high-climbing hapaxanthic (then always very short-stemmed) or pleonanthic, dioecious. Sheaths usually heavily armed with spines, the spines frequently highly organised. Flagellum absent. Knee frequently present. Leaves ecirrate in acaulescent species or longly cirrate. Leaflets variously arranged. Inflorescence male and female superficially similar, but within the genus of two basic types: one with all bracts enclosed within the outermost bract or prophyll, splitting along their length to expose the flowers (section *Cymbospatha*) or the other with bracts splitting along their entire length to leave no tubular portion and frequently falling (section *Piptospatha*). Bracts variously armed. Partial inflorescences longer than the subtending bract in section *Piptospatha*; bracteoles and "involucres" inconspicuous. Male rachilla bearing male solitary flowers, male flowers small, cup-shaped; calyx with three small lobes; corolla split to the base into 3 petals; stamen 6, slightly epipetalous; pistillode minute. Sterile male flower found with each female flower, as the fertile male, but stamens with empty anthers. Female rachilla bearing many flowers in dyads consists of one female flower and one sterile male flower. Female flower with calyx truncate or shallowly 3-lobed; corolla with 3 petals; gynoecium with 3 stigmas and with 3 loculi. Sterile flower smaller or at least more slender than the female ones, with well-formed calyx and corolla and 6 sterile stamens and an abortive ovary. Fruit variously shaped, tipped with stigmatic remains and covered with reflexed scales. Seed only one, covered by thin to thick, sweet or sour sarcotesta. Endosperm deeply ruminate. Embryo basal.

Distribution. Based on Dransfield et al. (2008), the geographical distribution of *Daemonorops* is more restricted than *Calamus*. The centre of distribution of both are similar, from China, India to New Guinea, specifically Sumatra, Malaya, Borneo and Malay Peninsula. *Daemonorops* does not occur in Africa, Himalaya, Peninsular India, Sri Lanka and Australia.

Habitat. Rather disturbed primary forest, on alluvial soil near rivers, flat to gently sloping terrain, ridge tops, lowland forest, and steep hill slopes in primary forest on volcanic soils.

Uses. One species is recorded to have sweet, edible young shoot (Mogea 1991).

Key to *Daemonorops* species in Sulawesi

1a. Leaf sheath covered with rusty-brown coloured indumentum and armed with short, up to 10 mm long, easily detached spines .... *D. takanensis*
1b. Leaf sheath without indumentum and armed with long, more than 15 mm long, strongly attached spines 2

2a. Leaf sheath armed with brittle, unequal, solitary (or groups of) spines 3
2b. Leaf sheath strongly armed with large, irregularly seriate spines 5

3a. Leaf sheath armed with solitary, black, brittle spines; ocrea present .... *D. lamprolepis*
3b. Leaf sheath armed with solitary (or groups of) black spines; ocrea absent 4

4a. Leaf sheath densely armed with very long, solitary, hair-like spines .... *D. sarasinorum*
4b. Leaf sheath armed with short, scattered, seriate, needle-like spines .... *D. riedeliana*

5a. Leaf sheath armed with oblique spines joined at their bases; fruit spherical, endosperm deeply ruminate .... *D. robusta*
5b. Leaf sheath armed with upright spines that are solitary or joined at their bases; fruit subglobose to ellipsoid, endosperm slightly to deeply ruminate 6

6a. Leaf sheath densely armed with solitary, furfuraceous spines; fruit ellipsoid, endosperm deeply ruminate .... *D. macroptera*
6b. Leaf sheath densely armed with greyish spines in groups of 3's to 5's; fruit subglobose, endosperm slightly ruminate .... *D. mogeana*

1. *Daemonorops lamprolepis* Becc., Rec. Bot Surv. Ind. 2: 223 (1902). TYPE: South East Sulawesi, Kendari, July 1874, *Beccari s.n.* (holo BO).

Clustering rattan. Sheathed stem up to 2 cm in diam., stem without sheath up to 1 cm in diam. Leaf sheaths green, covered with collar spines with jointed bases, scarcely up to 3 cm long, sheath surface smooth with caducuous reddish-blackish scaly indumentum, leaf sheath mouth armed as the rest of sheath; knee present, very conspicuous, armed as the rest of sheath; ocrea present, papery, small, to 5 mm high. Leaves to 3 m long including petiole 30 cm long, armed adaxially with short, erect, scattered spines to 2 mm long, abaxially armed with erect, very rarely solitary spines, up to 1 mm long; rachis unarmed, or armed only slightly proximally; cirrus up to 80 cm long, armed with regularly arranged groups of grapnel-like spines, leaflets mostly arranged regularly, 30 on each side of the rachis, stiff, horizontal; leaflets lanceolate, papery, acuminate, up to 30 cm long, 2 cm wide, armed with scattered reddish, short bristles along the main nerve on lower surface, transverse veinlets conspicuous. Female inflorescences pendulous to 37 cm long, peduncle 10–15 cm long, armed distally with groups of spines; prophyll papery, erect, 25 cm long, 3 cm wide, ellipsoid oblong, armed with scattered spines, some spines in groups of 2's; partial inflorescences up to 4, each inflorescence bearing up to 8 partial inflorescences; rachilla covered with chocolate scurf; involucre pendulous, flat, just above the involucrophore, 5 mm long; involucrophore short, papery, 2 mm long. Female flowers 6 mm long, ovoid, acute; calyx very short; the corolla several times longer than the calyx, ventricose at the base. Male inflorescence and male flowers unknown. Young fruits ovoid to ellipsoidal, 15 × 10 mm, covered by 8–9 vertical rows of encrusted scales. Seed ovoid, 10 × 7 mm, boldly tubercled and coarsely pitted. Endosperm ruminate.

Distribution. Donggala, Central Sulawesi and Kendari, South East Sulawesi.

Habitat and ecology. Disturbed primary forest.

Vernacular names. Rotan mapis (Donggala language), *lasero epe* or *lita* (Tobelo language).

Notes. This is the only species of *Daemonorops* from Sulawesi which has an ocrea. This ocrea is papery, small, to 5 mm high.

Specimens examined: **Central Sulawesi**: Northern central part, on the coast of South West of Donggala, 11 May 1975, *W. Meijer 10086*, fruiting (BO). Mountain Sojo, November 1913, *Rachmat 705*, fruiting (BO). **South Sulawesi**: Maliki, Desoe, 02 Jun 1933, *H.N. Reppie 18*, sterile (BO). Wadjo, *Heyne 2581*, *Heyne 2587*, sterile (BO); *Heyne 2615*, fruiting (BO); Boni, *Heyne 2599*, young fruit (BO); *Heyne 2595*, *Heyne 2604*, fruiting (BO); *Heyne 12*, dead female inflorescence (BO).

2. *Daemonorops takanensis* Rustiami, Reinwardtia 13(1): 25–30 (2009). TYPE: Indonesia, South Sulawesi, Kab. Mamuju, District Kaluku, Dusun Roa, Rantai Village, Kaluak, Bukit Takane-kane, 200 m alt., 06 February 1993, *Padmi Kramadibrata 28*, fruiting specimen (holo BO).

Slender, clustering rattan, climbing to 20 m. Sheathed stem 2 cm in diam., without sheaths 1.5 cm in diam., internodes 20–30 cm long; leaf sheath dark green, covered with conspicuously rusty brown-coloured indumentum and armed with numerous very brittle, thinly laminar, unequal, up to 1 cm long or even shorter, solitary, scattered, easily to detached, brown spines, with small bulbous bases; leaf sheath mouth densely armed with similar spines; knee present and conspicuous, 10 mm long, 20 mm wide, moderately armed. Leaves 3.5 m long including petiole and cirrus; petiole to 20 cm long, 10 mm wide and 8 mm thick at base, flat adaxially, rounded abaxially, with acute edges, covered slightly with rusty brown indumentum, as on sheath, armed with numerous short triangular spines; rachis up to 1.8 m long, armed with very short, erect, slender, triangular claws, that become ternate near the apex and 5-nate and half-whorled on the cirrus; cirrus to 150 cm long; leaflets numerous, 55 pairs on each side of rachis, regularly arranged, linear-lanceolate, acuminate, armed with bristles to 5 mm long along the midrib of both surfaces; transverse veinlets minute; basal leaflets 34 cm long and 8 mm broad, middle leaflets 35 cm long and 1 cm broad, apical leaflets to 20 cm long and 8 mm broad. Male and female inflorescences not known. Infructescence pendulous, up to 50 cm long, consisting of 4 partial infructescences, 5 cm apart; peduncle 10 cm long; partial infructescence to 8 cm long bearing 10 partial inflorescences. Fruit ellipsoid with a short conical beak, pale, covered with 15 vertical rows of scales, 15 mm long and 10 mm broad. Seed one, ellipsoid. Endosperm deeply ruminate.

Distribution. Known from the type locality only.

Habitat and ecology. Disturbed primary forest on hill slope.

Uses. Not recorded.

Vernacular name. Rotan api.

Notes. This species can be recognised easily by its dark green leaf sheath, covered with conspicuously rusty brown-coloured indumentum and armed with numerous very brittle, thinly laminar, unequal, up to 1 cm long or even shorter, solitary, scattered, easily to detached, brown spines, with small bulbous bases. So far this species is only known from the type locality, Bukit Takane-kane.

Specimens examined: **South Sulawesi**: Kab. Mamuju, District Kaluku, Dusun Roa, Rantai Village, Kaluak, Bukit Takane-kane, 200 m alt., 06 Feb 1993, *Padmi Kramadibrata 028*, fruiting specimen (BO).

3. *Daemonorops macroptera* (Miq.) Becc., Rec. Bot. Surv. Ind. 2:223 (1902); *Calamus macropterus* Miq., Verh. Kon. Akad. Wetensch., Afd. Natuurk. 11 (5): 19 (1868); *Palmijuncus macropterus* (Miq.) Kuntze, Revis. Gen. Pl. 2: 733 (1891). TYPE: North Sulawesi, Manado, Minahasa, *Riedel IGF s.n.* (holo BO; iso L).

Clustering robust rattan, up to 40 m tall. Leaf with sheaths up to 3 cm in diam., without sheaths to 2 cm in diam., sheaths covered with basally joined robust spines, up to 5 cm long, leaf sheath mouth armed as the rest of the sheath; knee present conspicuously, armed as the rest of the sheath. Leaves up to 6 m long including petiole to 40 cm, armed with groups of robust spines, to 2 cm long, on both surfaces; rachis armed with scattered, solitary spines up to 1 cm long; cirrus more than 2 m long, armed with regularly arranged groups of very robust grapnel-like spines, blackish at the tip; leaflets mostly arranged regularly, slightly irregular apically, 70 on each side of the rachis, stiff, horizontal; leaflets lanceolate, papery, acute, up to 55 cm long, 3 cm wide, armed with scattered, reddish, short bristles along the main nerve on lower surface, up to 1 cm long, short bristles along the leaflets margin; transverse veinlets very minute, and sharp. Male inflorescence pendulous, up to 85 cm long including peduncle 25–30 cm long, peduncle straight and rigid, flattened, densely armed with flat, irregular, erect, spreading, 1–2 cm long spines; the outer bract is narrowly lanceolate before flowering; after flowering it is coriaceous, gradually narrow to acuminate, covered with furfuraceous indumentum; rachilla about 40 cm long, with 5 small partial inflorescences. Male flower small, 4–5 mm long; calyx very small, deeply 3-dentate. Female inflorescence elongate, rather slender, pendulous up to 65 cm long, bearing 6–7 partial inflorescences; secondary spatha short, acute or acuminate, up to 8 cm long, covered with rusty indumentum. Female flower unknown. Infructescence pendulous, to 60 cm long, peduncle up to 15 cm long, armed distally with groups of robust spines; peduncular bracts leathery, erect 25 cm long, 3 cm wide, ellipsoid oblong, covered by rusty indumentum, armed with solitary spines up to 2 cm long, partial inflorescences 5 each, bearing up to 9 partial inflorescences; involucre pendulous, flat, just above the involucrophore, 5 mm long; involucrophore short, papery, 2 mm long. Fruits obovoid, 15 × 15 cm, covered by 7 vertical rows of encrusted scales. Seed ovoid, 10 × 10 mm, smooth surfaces.

Distribution. North and Central Sulawesi.

Habitat and ecology. Rather disturbed primary forest, on alluvial soil near river, terrain flat to gently sloping.

Vernacular name. Rotan batang, angah.

Notes. This rattan, based on Vogel's field record, produces a white gummy exudate from the cut stem and the immature fruit is green. It is found at low elevations along river terraces (field note of *Musser* T10).

Specimens examined: **North Sulawesi**: Manado, *Miquel s.n.*, fruiting (BO, L). **Central Sulawesi**: Sopu Valley, c. 80 km SSE of Palu, 1000 m alt., 2 May 1979, *E.F. de Vogel 5171*, fruiting (BO); 22 May 1979, *E.F. de Vogel 5508*, fruiting (BO); 26 Apr 1979, 1000 m asl., *E.F. de Vogel 5055*, fruiting (BO, K); Mountain Rorokatimbu, 13 May 1979, *E.F. de Vogel 5326*, fruiting (BO, K); Poso, Lore Utara, Gn. Pada Esa, 11 Sep 2010, 1525 m asl., *Himmah Rustiami, Dewi, M. Amir, Hamzah & Ato HR 447*, fruiting material, Mt. Petulu, Kulawi, 18 Feb 1986, 700 m asl, *Anggana & Yusuf Dali 62*, sterile (K); Sungei Tolewonu, 30 km South of Kuala Navusu, between 1974–1976, *G.G. Musser T10* (K). **South East Sulawesi**: Tongoa, 730 m asl., 4 Mar 1981, *J.Th. Johansson, H. Nybom & S. Riebe 169* (K).

4. *Daemonorops mogeana* Rustiami, Reinwardtia 13(1): 25–30 (2009). TYPE: Indonesia, Central Sulawesi, Kab. Poso, District Kulawi, Dusun Moa, Mt. Malemo, 1000 m alt., 21 October 1977, *JP Mogea 1356*, fruiting specimen (holo BO; iso K, L).

Very large, robust, clustering rattan, climbing to 15 m. Sheathed stem 4 cm in diam., stem without sheaths 2 cm in diam.; internodes 20 cm long. Leaf sheaths woody, creamy-yellow, densely armed with numerous broad spines often with conspicuous bulbous bases, and arranged in groups of 3's to 5's, flat, greyish, irregularly seriate, 1–7 cm long, 5 mm wide, intermixed with smaller and ascendant spines. Leaves very large, up to 6 m long including petiole and cirrus; petiole very robust, 1 m long, 2 cm wide and 1 cm thick at base, rounded adaxially and abaxially, densely armed with, seriate or irregularly, erect, triangular, 1–3 cm long and up to 1 cm wide spines; rachis up to 3 m long, with similar triangular spines; leaflets large, 30 pairs on each side of rachis, regularly arranged, linear-lanceolate, acuminate, armed with small bristles, 5 mm long along the mid nerve on both surfaces and the apex; transverse veinlets conspicuous; middle leaflets 40 cm long; 2 cm broad, papyraceous, green and concolorous; apical leaflets to 20 long, 1.5 cm broad; cirrus to 2 m long, armed with 4–5 hooked grapnels arranged 3 cm apart. Male and female inflorescences not known. Infructescence ascending, to about 70 cm long, with 6 erect, very slender, cupressiform, partial infructescences, 5 cm apart; the main axis cylindrical, 20 cm long, armed with dense, glaucous, seriate spines, about 1–5 cm long, with bulbous bases, and covered with blackish brown indumentum; partial infructescence about 15 cm long, bearing up to 10 unequal secondary partial infructescences. Fruit subglobose, covered with 14 vertical rows of glossy yellowish scales, 8 mm long and 4 mm broad. Seed one, globose. Endosperm slightly ruminate.

Distribution. Known from type locality only.

Habitat and ecology. This species is common in *Agathis* forest, beside streams on the slopes of G. Malemo, 1000 m alt.

Distribution. This species is only known from the type locality.

Uses. Young shoot is edible and good.

Vernacular name. Uwi manis (*umbut manis*).

Notes. This species has been identified by Maturbongs (*in scheda*) in 2001 as *Daemonorops macroptera*, to which it is morphologically similar. However, after careful examination, *D. mogeana* differs from *D. macroptera* by the leaf-sheath armature which includes very robust spines, subglobose fruit and slightly ruminate endosperm. In contrast, *D. macroptera* has gigantic, fragile, easily broken spines, and ellipsoidal fruit and deeply ruminate endosperm.

Specimen examined: **Central Sulawesi**: Kab. Poso, District Kulawi, Dusun Moa, Mt. Malemo, 1000 m alt., 21 October 1977, *J.P. Mogea 1356*, fruiting specimen (BO, K, L).

5. *Daemonorops robusta* Warb. ex Becc., Ann. Roy. Bot. Gard. (Calcutta) 12(1): 101 (1911). TYPE: Bojong, Province Minahasa, North Sulawesi, *Warburg s.n.* (Herb. Berlin, *n.v.*, probably destroyed, type specimen pictures seen in Beccari's book kept at K).

Solitary to clustering rattan, very robust, 5–7 m tall. Leaf with sheath 7 cm in diam., without sheath 2–3 cm in diam.; internodes 15–35 cm long. Leaf sheaths pale yellow-green, covered with oblique, very large black thorns with joined bases up to 5 cm long, sheath surface with caducous glaucous black indumentum, leaf sheath mouth armed as the rest of sheath; knee present conspicuously, armed as the rest of sheath. Leaves to 4 m long including petiole to 40 cm long, armed adaxially with densely erect, long black spines to 5 cm long, abaxially armed with erect, oblique spines in groups up to 5 cm long; rachis armed with erect, solitary spines up to 5 mm long; cirrus up to 150 cm long, armed with regularly arranged groups of grapnel-like spines, blackish at the tip; leaflets lanceolate, papery, acute, 60 cm long, 2 cm wide, armed with scattered reddish, short bristles along the main nerve on the lower surface, leaflet margin armed with short spinules, reddish. Male inflorescence ascending, to 50 cm long, peduncle up to 22 cm long, armed with groups of 2–8 slightly bulbous based spines 2–20 mm long with pointed tips, more robust adaxially than abaxially; peduncular bract woody, erect to 48 cm long, 4 cm wide, lanceolate at the tip, covered by rusty brown indumentum. Female inflorescence not known. Infructescence pendulous, 50–100 cm long, peduncle 20–30 cm long, armed with spines forming rings; peduncular bracts leathery, erect, 30 cm long, 2 cm wide, ellipsoid oblong, covered by rusty indumentum, armed with scattered needle like, blackish spines; partial inflorescences 5–6, each bearing up to 8 secondary partial inflorescences; involucre pendulous, flat, just above the involucrophore, 5 mm long; involucrophore short, papery, 2 mm long. Fruits spherical, 15 × 10 cm, covered by 9 vertical rows of yellowish cream encrusted scales. Seed globular, 8 × 8 mm, seed surface reticulate, endosperm deeply ruminated.

Distribution. North Sulawesi: Bolaang Mongondow, Manado, Laelumbuan; Central Sulawesi: Toli-toli.

Habitat and ecology. Primary forest hillslopes, deep valleys, alluvial flats, lowland riverbank forest.

Vernacular names. Lauro manu (*toli-toli*), *pondas valukan, pondas rasisagan, pondas kuluwi* (Manado), *rotan susu* (Gorontalo language).

Notes. The mature fruit of this species has a sour sarcotesta; the young fruit is green, maturing red. Apparently related to *D macroptera* but the fruit is spherical.

Specimens examined: **North Sulawesi**: Bolaang Mongondow, Tapak Kulintang, Dumoga Bone National Park, 220 m alt., 8 Mar 1984, *J.P. Mogea JPM 5076*, young fruit (BO, K). Bolaang Mongondow, Pindol, Lolak, 50 m alt., 19 Oct 1973, *J. Dransfield & J.P. Mogea JD 3805*, mature fruit (BO); JD 3800, male flower (BO, K). Manado, Pondok Pingsang, Karoewatoe, 50 m alt., 26 Feb 1895, *Koorders KDS 18410β*, fruiting (BO, L); Laelumbulan by Paku Ure, 700 m alt., 9 Mar 1895, *Koorders KDS 18399β*, fruiting (BO, L). *Heyne 2510*, sterile (BO); Gorontalo, near Marisa, Illoheleuma, 8 Jan 1989, *Lynn Clayton 3*, fruiting (K). **Central Sulawesi**: Dako, Mountain Lakatan, Toli-toli, 750 m alt., 25 Feb 1985, *Ramlanto & Z. Fanani 530*, fruiting (BO). Malili, Toli-toli, Kawata, 200 m alt., 13 Apr 1933, *J. van Jijll de Jong 1*, young fruit (BO); Inland from Batui and Seseba on Batui river, Sinsing, 16 Oct 1989, 70–100 m asl., *Coode 5967*, fruiting (K).

6. *Daemonorops riedeliana* (Miq.) Becc., Rec. Bot. Surv. Ind. 2:226 (1902); *Calamus riedelianus* Miq., Verh. Kon. Akad. Wetensch., Afd. Natuurk. 11: 18 (1868); *Palmijuncus riedelianus* (Miq.) Kuntze, Revis. Gen. Pl. 2: 733 (1891). TYPE: North Sulawesi, Manado, Minahasa, 1895, *Riedel s.n.* (holo L).

Slender, clustering rattan, up to 10 m tall. Stem with sheaths up to 20 mm in diam., without sheaths to 6 mm in diam., internodes 8–10 cm long; leaf sheaths covered with needle-like, almost uniformly upward-pointing spines that are solitary or in groups, the spines enormous, up to 6 cm long; sheath surface smooth with corky creamy indumentum; leaf sheath mouth armed as the rest of the sheath; knee present conspicuously, armed as the rest of the sheath. Leaves to 2 m long including petiole to 15 cm, armed very densely with 5–10 mm long spines all around, lower side of rachis armed with ternate claws, upper side slightly prickly; leaflets numerous, arranged rather distantly, 38–57 pairs on each side of the rachis, arcuate, somewhat spidery; leaflets lanceolate, papery, acuminate, 25–30 cm long, 1 cm wide, armed with scattered, reddish, bristly spinules along the mid-nerve of the upper surface; young leaf covered in caducous white indumentum; transverse veinlets slender, visible on both surfaces; margins armed with rather close ciliate spines,. Male and female inflorescences not known. Fruits spherical, 13 × 13 mm, covered by 8 vertical rows of yellowish brown, dull encrusted scales. Seed irregularly globular, 10 × 8 mm, with reticulate surface.

Distribution. North and South Sulawesi.

Habitat and ecology. Disturbed primary forest, and steep hillslopes and ridge top lowland forest, on volcanic soil, 500 m asl.

Vernacular name. Angah (this name is also applied to *D. macroptera*).

Notes. It is noted by Dransfield that the seed is both astringent and sweet.

Specimens examined: **North Sulawesi**: Minahasa, Bitung, Batu Angus Nature Reserve, 500 m alt., 7 Oct 1973, *J. Dransfield & J.P. Mogea JD 3737*, fruiting (BO); Bolaang Mongondow, Pindool Lolak, 150 m alt., 18 Oct 1973, JD 3787, male flower (BO, K); Manado, 2 Mar 1895, *Koorders 18389β*, fruiting (BO, L); *A.G. Waturandang 51*, sterile (BO). **South Sulawesi**: Kabupaten Mamuju, Kec. Kaluku, Dusun Roa, Desa Dutas Kaluak, Bukit Banga, 300 m alt., 08 Feb 1993, *Padmi Kramadibrata 30*, sterile (BO).

7. *Daemonorops sarasinorum* Warb. ex Becc., Ann. Roy. Bot. Gard. (Calcutta) 12 (1): 100 (1911). TYPE: North Sulawesi, Tomohon, in the province of Minahasa, *Sarasin 1082* (Herb. Berol., *n.v.*, probably destroyed, type specimen pictures seen in Beccari's book kept in K).

Robust, clustering rattan, climbing 15–30 m long. Stem with sheath 6 cm in diam., without sheath to 4 cm in diam.; internodes generally rather short, 20 cm long. Leaf sheath very densely covered in reflexed black spines, to 4 cm long, pinkish when young; sheath surface with buff scurfy sometimes variously grey indumentum, leaf sheath mouth armed as the rest of sheath; knee present, very conspicuous, armed as the rest of sheath. Leaves 2.5–4 m long including petiole 40 cm or more, the petiole somewhat reddish, armed adaxially with short, erect, scattered spines to 4 mm long, abaxially armed with erect, solitary spines rarely up to 15 mm long; rachis unarmed or proximally only slightly armed; cirrus up to 2 m long, armed with regularly arranged groups of grapnel-like spines, blackish at the tip; leaflets mostly regularly arranged, densely crowded, 50–75 on each side of the rachis, stiff; leaflets lanceolate, papery, acuminate, 60–80 cm long, 2 cm wide, armed with scattered, reddish short bristles along the main nerve on both surfaces. Male inflorescence pendulous, up to 120 cm long, consisting of 15 rachillae, each rachilla consisting of 8 partial inflorescences; peduncular bract narrow and elongate, cupressiform with several erect, compact or appressed flowers; partial inflorescence covered with abundant furfuraceous indumentum. Male flowers short, 4 mm long, with anthers quite exserted from corolla and enclosed within spathes; calyx is very small, almost flat, corolla is longer than calyx. Female inflorescences pendulous, 60 cm long, peduncle 20 cm long, densely armed with groups of spines; peduncular bract leathery, elongate, 17 cm long, 3 cm wide, cupressiform, covered with rusty indumentum and innumerable long, narrow, scattered black spines, tubular before flowering; partial inflorescences 6, each bearing up to 11 secondary partial inflorescences; involucre pendulous, flat just above the involucrophore, 5 mm long; involucrophore short, papery, 2 mm long. Female flowers at the time of anthesis 4 mm long, exclusive of the stigmas which are exserted from the corolla and are about as long as the whole length of the female flowers (c. 8 mm); calyx very short, copular, polished (not striate), superficially 3-toothed; corolla ventricose, urceolate, strongly seriately veined, coriaceous, having 3 broadly triangular, acute teeth.

Distribution. North Sulawesi: Manado, Bitung, Kotamobagu; Central Sulawesi: Palu, Mt. Rorokatimbu.

Habitat and ecology. Montane forest, somewhat disturbed lower montane forest on steep terrain, shallow clayey soil.

Vernacular name. Pondan katunun (Manado).

Notes. Male flowers are unpleasantly ester-scented (from *JD 3862*).

Specimens examined: **North Sulawesi**: Manado, Minahasa 2 Mar 1895, *Koorders KDS 18391β*, sterile (BO); 30 Apr 1895, *Koorders KDS 18407β*, sterile (BO). Minahasa, Bitung, Batu Angus Nature Reserve, 800 m alt., 8 Oct 1973, *J. Dransfield & J.P. Mogea JD 3744*, fruiting (BO). Bolaang Mongondow, G. Ambang, Kotamobagu, 1000 m alt., 26 Oct 1973, JD 3862, male flower (BO, K); JD 3861, fruiting (BO, K). Manado, Pondok Simpang, 50 m alt., 2 Mar 1895, *Koorders KDS 18388β*, sterile (BO). **Central Sulawesi**: Mt Rorokatimbu, west slope c. 80 km SSE of Palu, 1700 m alt., *E.F. de Vogel 5484*, female flower (BO, K); 13 May 1979, c. 1°16'S 120°18'E, 1300 m alt., *E.F. de Vogel 5335*, sterile (BO, K); Mount Sadaunta, May 1976, *G.G. Musser* s.n., (K).

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The Pandanaceae of the Bukit Baka Bukit Raya National Park and adjacent areas, West and Central Kalimantan, Indonesia, with notes on their nomenclature and the rediscovery of *Pandanus aristatus* and several new records

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ABSTRACT. Eight species of Pandanaceae (3 *Freycinetia* spp., 5 *Pandanus* spp.) were recorded from the Bukit Baka Bukit Raya National Park and adjacent areas in the West and Central Kalimantan Provinces, Indonesia. *Pandanus aristatus* was recollected and the description improved. *Pandanus motleyanus* has been assigned to synonymy under *P. yvanii*. *Pandanus yvanii* and *P. helicopus* were found to occupy different niches in the peat swamps. *Pandanus epiphyticus* Martelli and *P. pachyphyllus* Merrill were recorded for the first time in Kalimantan. The doubtful presence of *F. sumatrana* in Java is resolved. Two Eastern Malesian species, *F. amboinensis* and *F. ceramensis* are synonyms of *F. sumatrana*, thus the species is now an exceptionally widespread species in both western and eastern Malesia. Full descriptions of species are provided.

Keywords. Borneo, Bukit Baka Raya, *Freycinetia*, Kalimantan, Pandanaceae, *Pandanus*

Introduction

The *pandan* flora of Borneo has been studied by Stone (1970a, 1993). Most of the species enumerated were from Sarawak and Sabah and little was known from Kalimantan, the Indonesian part of Borneo, particularly from the southwestern part, where the Bukit Baka Bukit Raya National Park is located.

Bukit Baka Bukit Raya National Park is a protected area within the Schwaner Range on the border between the Indonesian Provinces of West and Central Kalimantan, with an area of approximately 181,090 hectares. Prior to this study, the latest *pandan* collecting activity in the vicinity was by Nieuwenhuis in the western and central parts of Kalimantan (Nieuwenhuis 1898, Steenis 1950). The *pandan* collections collected during the Nieuwenhuis expedition were identified by Martelli and later mentioned in his two enumerations (Martelli 1910, 1913). Merrill (1922) and Martelli (1929) also cited these expedition specimens in their accounts on the *pandan* of Borneo, in which many of the collections had been appointed as types.

Although numerous publications have been produced since (see Kanehira 1938; St. John 1961, 1965; Stone 1967a, 1967b, 1970a, 1978, 1980, 1982, 1983b, 1993), the *pandan* flora of the Bukit Baka Bukit Raya National Park and surrounding areas was hardly mentioned and still made reference to Martelli (1929). Only *Pandanus aristatus* was mentioned for the National Park (Stone 1993). The most recent expedition carried out within the National Park was the 1982–1983 expedition in Bukit Raya conducted by Reuler (1987), when no *pandan* was collected.

This paper describes several species of the pandan flora in the Bukit Baka Bukit Raya National Park and adjacent areas, including the Gunung Kelam Ecopark and Baning Protected Forest, based on the most recent expedition in 2006, as well as observations made with herbarium specimens kept in the BO Herbarium.

Enumeration of species

Freycinetia

1. *Freycinetia kartawinatae* A.P. Keim, Reinwardtia 13(1): 15 (2009). TYPE: *A.P. Keim 770* (holo BO!), Indonesia, West Kalimantan, Katingan Hulu, Waringin Timur, on logging road, 2 May 2006. (Fig. 1)

Robust climbing *pandan*, to 50 m high. *Stem* c. 9.5 cm girth (c. 3 cm diameter). *Leaves* spirally arranged in 3 ranks (tristichous); blade lanceolate-elongate, c. 43.5–44 cm long, c. 3 cm wide, apex acuminate, margin with spines up to distal 1/3 of the length; adaxial surface green, glabrous; abaxial surface pale green, glabrous; auricle tapered, margin entire, brownish yellow to creamy brown; leaf sheath yellowish green. *Infructescence* terminal, c. 14 cm long, consisting of 3 to 4 spirally arranged cephalia; pedicel yellow to pale yellowish orange, glabrous; bracts distinctively bright orange, thick, hard, fleshy, glabrous, apex acuminate, margin with spines, each boat shaped, c. 22.5–23 cm long, caducous. *Cephalium* cylindric-elongate, c. 9 cm long, c. 3 cm wide, pale green to dull greyish green; stigma 4–5, mostly 4.

Distribution. Endemic to Kalimantan.

Habitat. Lowland tropical rain forest at about 300 m altitude.

Vernacular names. Kajak rajak, *mèrajak* (Dayak, Belaban dialect).

Uses. Although not used by local people, orang utans and gibbons are said to consume the bracts.

Notes. In general appearance, *F. kartawinatae* is very similar to *F. insignis*, but differs in its orange infructescence bracts compared to the purplish white bracts in *F. insignis*.

Fig. 1. *Freycinetia kartawinatae* A.P. Keim. **A.** A terminal infructescence with four spirally arranged cephalia and very distinctive bright orange bracts (above). **B.** Terminal infructescence with three spirally arranged cylindric-elongate cephalia with yellow glabrous pedicels, the bracts already fallen away (below). Photos: A.P. Keim, Rugayah & H. Rustiami.

Among members of the section *Polystachya* in Borneo that have infructescences with 3 cephalia or more, *F. kartawinatae* differs from *F. kinabaluana* in its terminal infructescences with 3–4 cephalia, compared to the lateral infructescences of *F. kinabaluana* that have 5–6 cephalia per infructescence. *Freycinetia kuchinensis* also has reddish orange bracts, but differs in having 2–3 cephalia per infructescence (*fide* Martelli 1910) that are globose, compared to the 3–4 cylindric-elongate cephalia per infructescence in *F. kartawinatae*. Although it has similarly long (40–60 cm) leaves and also 3–4 stigmas, *F. sarawakensis* differs from *F. kartawinatae* in its lateral (not terminal) infructescences and scabrid (not glabrous) pedicels.

A taxon from Sarawak would appear to have many similarities with *F. kartawinatae*, especially in having orange bracts, terminal infructescences, and 3–4 cephalia per infructescence. This taxon was named *F. andersoniana* by Stone (1967c), but invalidly published.

Specimens examined: Only known from the type.

2. *Freycinetia sumatrana* Hemsley, J. Linn. Soc. Bot. 30: 167 (1894). TYPE: *Beccari 211* (holo K; iso FI), Indonesia, Sumatra, Mount Singalan (presumably Mount Singgalang in West Sumatra), June 1878. (Fig. 2–5)

Freycinetia valida Ridley, Mat. Fl. Mal. Penins. 2: 234 (1907). LECTOTYPE: *Ridley 3937* (SING!), Malaysia, Malay Peninsula.

Freycinetia auriculata Merrill, Philipp. J. Sci., C. Bot. 3: 312 (1908). TYPE: *Bur. Sci. Foxworthy 876* (holo PNH†; iso A), Philippines, Palawan, Puerto Princesa, May 1906.

Freycinetia loheri Martelli, Webbia 3: 15 (1910). SYNTYPES: *Loher 1577* (K; iso PNH†), Philippines, Luzon, Benguet, 1908–1915; *Loher* 1578; *Loher* 5469, Luzon, Montalban, June 1908–1915.

Freycinetia lucida Martelli, Webbia 3: 168 (1910). TYPE: *H. Hallier 3188* (holo BO!; iso L), Indonesia, Kalimantan, Amai-Ambit, 1893–1894.

Freycinetia ceramensis Martelli, Webbia 3: 169 (1910). TYPE: *G.H. de Vriese s.n.* (holo L), Indonesia, Moluccas, Seram, 1857–1861.

Freycinetia amboinensis Martelli, Webbia 3: 170 (1910). TYPE: *Teysman s.n.* (holo BO! iso L), Indonesia, Moluccas, Ambon.

Freycinetia sumatrana Hemsley var. *penangiana* B.C.Stone, Gard. Bull. Singapore 25(2): 202 (1970). TYPE: *Stone5890* (holo KLU), Malay Peninsula, Selangor, Templer Park, Kanching, June 1965.

Robust climbing *pandan*, to 20 m high. *Stem* 7–8 cm girth. *Leaves* spirally arranged in 3 ranks (tristichous); blade lanceolate-elongate, apex acuminate, margin with spines throughout, 60–135 cm long, 2.5–3.5 cm wide; adaxial surface green, glabrous; abaxial surface pale green, glabrous; auricle lobed, margin entire, pale purplish red to pale brownish yellow; leaf sheath white, purplish red in young leaf. *Infructescence* terminal, consisting of 3–4 spirally arranged cephalia. *Cephalium* elongate, 16–19 cm long, green to yellowish green; stigmas 2–4, mostly 2; pedicel 9–10 cm long, glabrous, pale yellowish green.

Distribution. Andaman Islands, Malay Peninsula, Sumatra, Java, Borneo, the Philippines, and Moluccas.

Habitat. Lowland tropical rain forest. In Bukit Baka Bukit Raya National Park commonly found at elevations lower than 500 m (Fig. 2). One specimen (*F.H. Endert 3875*, BO!) was collected from Mount Kemoel in East Kalimantan at 1200 m.

Vernacular names. *Rajak* (Dayak, Balaban dialect).

Uses. Leaves are used for baskets, mats and handicrafts.

Notes. The differences between *F. sumatrana* and the taxa listed above in the synonymy are slight and merely in leaf dimensions, cephalia size, colour of bracts, appearance of auricles, pedicel surface, and stigma number.

The possession of lobed auricles is a more important feature that distinguishes this species, as acknowledged previously by Stone (1968), who newly proposed the section, *Auriculifoliae* based on this character. A year later, Stone (1969) excluded *F. loheri* and *F. vidalii* from the section based on the fact that neither of these two species actually possessed lobed auricles. In the same publication *F. auriculata* was placed as a synonym of *F. sumatrana*. Finally, *F. valida* was included into synonymy (Stone 1970a).

The present study supports Stone in placing *F. auriculata* and *F. valida* as synonyms of *F. sumatrana*. Despite no information concerning bract colour and the relatively smaller size of the cephalium, there is no significant difference between *F. auriculata* and *F. sumatrana*.

For *F. valida*, Ridley (1907; 1925) did not mention anything about the bract colour. Only a brief note on the female bract was given, which was described as leaf-like and not coloured. We interpret "not coloured" as white, so that is not different from *F. sumatrana*. Actually, Ridley (1925) himself noted that *F. valida* is very near to *F. sumatrana*.

Regardless of the immature state of the cephalia, the observations made on the types indicate that there is no single decisive morphological character that can be used to distinguish *F. amboinensis* or *F. lucida* from *F. sumatrana*.

The placement of *F. amboinensis* as synonym has a further consequence that *F. sumatrana* is now found in the Moluccas, particularly in Ambon and Halmahera

Fig. 2. *Freycinetia sumatrana* Hemsley from Bukit Baka Bukit Raya National Park. **A.** Robust habit with terminal infructescence. **B.** Infructescence of four elongate-ellipsoidal cephalia. Photos: A.P. Keim, Rugayah & H. Rustiami.

Islands; thus new records of *F. sumatrana* for the two islands. The presence of *F. sumatrana* in the Moluccas is also supported by the placement of *F. ceramensis* into its synonymy. Although *F. ceramensis* possesses auricles with more pronounced spines (Fig. 3), this is insufficient for distinction from *F. sumatrana*. Observations made on specimens recently collected from Seram, an island within the Moluccas Archipelago just north of Ambon (Keim et al. 2008) indicate that the spines vary from minute to apparent even in the same branch. Auricles with minute spines are usually observed on younger leaves (i.e., the terminal part of the branch), whereas auricles with larger spines are found on older leaves. Prior to this placement *F. ceramensis* was known as an endemic of Seram Island; so now *F. sumatrana* is also newly recorded for the island.

The placement of two Eastern Malesian species (*F. amboinensis* and *F. ceramensis*) into the synonymy of *F. sumatrana* has the consequence that the species is now recognised as one of the most widespread species of the genus in Malesia, occupying both western and eastern parts. The other such species is *F. scandens*.

Stone (1970b) described the smaller overall dimensions and "entire auricle" as two important characters that distinguish *F. lucida* from *F. sumatrana*. That description of the auricle does not agree with the protologue (Martelli 1910) that clearly described the auricle as with minute spines (original text: "*ad margines crebre et minute fimbriato-denticulatis*"). The present study is in favour of Martelli; thus, the possession of spiny auricles helps place *F. lucida* in the synonymy of *F. sumatrana*.

Stone (1970a) identified a specimen collected from the top of Mount Beratus (altitude 1200 m) in South Kalimantan, *W. Meijer 904* (BO! with duplicate at L) as *F. lucida*. This specimen has now been determined as *F. sumatrana*, and marks the first record of *F. sumatrana* in the Indonesian part of Borneo (Kalimantan). The collections made in this present study support the identification of the species in Kalimantan. Previously *F. sumatrana* was only known from Sarawak and Sabah (Stone 1970a). As a consequence, *F. sumatrana* is now known to be more widely distributed throughout Borneo. A specimen (*F.H. Endert 3875*) was also collected from 1200 m, and in Sumatra and the Malay Peninsula, the species can still be found at an altitude of approximately 1828 m (Stone 1970b).

The varietal status of *F. sumatrana* var. *penangiana* is not accepted as the slight differences in the shape and colour of the auricles mentioned by Stone (1970b) are regarded as insufficient distinction, based on observations from the Bukit Baka Bukit Raya National Park. The specimens clearly show that auricles can vary from tapered to lobed even in the same shoot (Fig. 4). There is also variation in auricle colour from bright purplish pink to light brownish yellow. Actually the variation in the type of auricle in *F. sumatrana* is not unusual.

An infructescence with 4 cephalia observed in one of the collections made for this study (*A.P. Keim 764*, BO!; Fig. 2) raises the possibility that this could be a member of the section *Polystachya*, which in Borneo is represented by a single known species, *F. kinabaluana* (Stone 1970a). However, the specimen clearly possesses a lobed auricle, a feature that is completely absent in *F. kinabaluana*. *Freycinetia kinabaluana*, on the other hand, has a lateral infructescence consisting of 5–6 cephalia. *Freycinetia*

Fig. 3. *Freycinetia ceramensis* Martelli, just recently rediscovered and collected from Ceram Island in the Moluccas (Keim et al. 2008). **A.** Robust habit and climbing to more than 20 m high. **B.** Ternate staminate inflorescences (the bracts are pale yellow and basally tinged reddish purple) that are obviously simlar to those of *F. sumatrana*. **C.** Infructescences, here binate but mostly ternate. **D.** The distinctive lobed auricles with spines on the margins. The characters shown in these pictures are regarded as clearly supporting the placement of *F. ceramensis* into the synonymy of *F. sumatrana*. Photos: A.P. Keim & S. Susiarti.

sumatrana always has terminal infructescences and has never been reported having more than 4 cephalia in one infructescence. Stone (1970c) notes that *F. sumatrana* in the Malay Peninsula has 3–4 cephalia per infructecence, and we know of at least one collection with 4 cephalia, *Endert 3875* (BO! duplicate at L), which was collected from Sumatra.

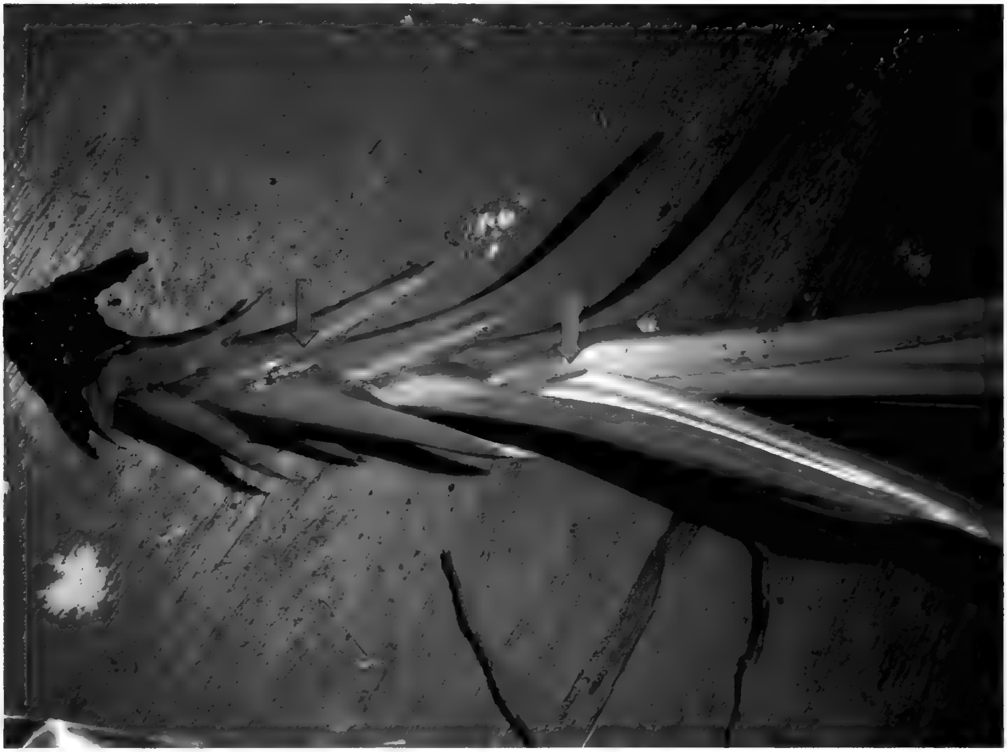

Fig. 4. Auricle variation in *F. sumatrana* from Bukit Baka Bukit Raya National Park. Tapered (left arrow) and lobed (right arrow) auricles can be found in the same young shoot (auricles are purplish pink in fresh specimens, but on mature branches or stems, brownish yellow ones are more common). Photo: A.P. Keim, Rugayah & H. Rustiami.

Numerous specimens from Java kept in BO that were previously labelled *F. valida* had been identified by Stone as *F. sumatrana*. Based on this, Stone (1972) suggested the presence of the species in Java. The same specimens have been re-identified in the present study as belonging to *F. insignis* based on the fact that none of those specimens actually has the distinctive lobed auricle and information from the fieldnotes clearly mentioned deep red or pale purplish red bracts, a feature that is characteris of *F. insignis*.

The presence of the true auriculate *F. sumatrana* in Java was finally proven based on collections recently made in the Gunung Tukung Gede Nature Reserve in Banten, western Java (*T. Djarwaningsih 1499*; Djarwaningsih pers. comm., 2010; Fig. 5). This is expected, as the islands of Java and Sumatra are only separated by the

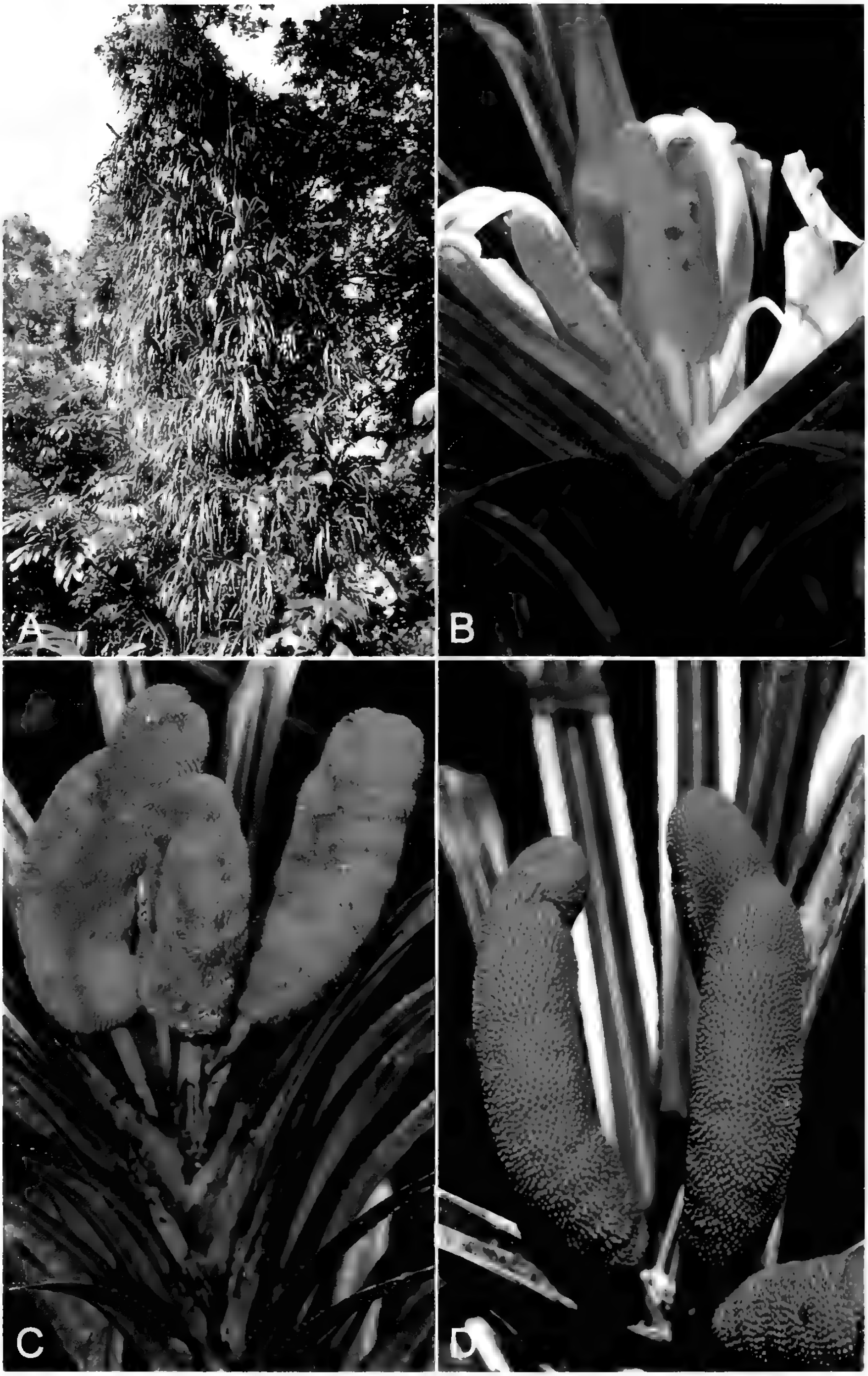

Fig. 5. *Freycinetia sumatrana* Hemsley from the Gunung Tukung Gede Nature Reserve in Banten, western Java. **A.** Habit. **B.** Young terminal ternate infructescence with the characteristic creamy white-pale yellow bracts with reddish purple-tinged basal part. **C.** Mature terminal ternate infructescence showing the distinctive lobed auricle. **D.** Young terminal quaternate infructescence, not uncommon in *F. sumatrana*. Photos: T. Djarwaningsih & A. Supriatna.

relatively narrow Sunda Strait.

Freycinetia walkeri shares many morphological similarities with *F. sumatrana*, particularly the lobed auricle and the number of stigmas. Indeed, other than the colour of the bracts, there is no substantial difference between this species and *F. sumatrana*. Stone (1975) mentioned that *F. walkeri* differs from *F. sumatrana* only in the smaller size of the cephalium (Stone wrote "fruits") and red floral bracts. Solms (1878) did not mention bract colour and it was Stone (1969; 1975) who mentioned the red bract colour based on observations he made on several non-type specimens, particularly *N. Wirawan 818*.

The BO Herbarium has two specimens identified by Stone (1975) as *F. walkeri*, *N. Wirawan 818* (BO!) and *Kostermans 24071* (BO!). *Wirawan 818* is a staminate collection from the vicinity of Ratnapura, Ceylon in 1969, in which the bract colour is noted as bright red, while *Kostermans 24071* (collected also in Ratnapura vicinity, Ceylon in 1973) is a pistillate collection with a fieldnote mentioning the fruit as dark red. Stone did visit Ceylon, but mostly worked in the Peradeniya Botanic Garden, thus he had never seen or collected *F. walkeri* in the field and was apparently using only specimens and citing from fieldnotes. The result of this current study is not in accordance with Stone in recognising the two specimens as *F. walkeri*. Neither has the distinctive lobed auricle, and the specimens are unlikely to be *F. walkeri*. Therefore, Stone's description of the bract colour in *F. walkeri* as red is considered doubtful. Until better specimens become available *F. walkeri* is regarded as a distinct species but closely allied to *F. sumatrana*. Further study is still required. When the matter of bract colour is resolved, *F. sumatrana* is likely to become a synonym of *F. walkeri* based on the law of priority.

Specimens examined: INDONESIA. **West Kalimantan**, Amai-Ambit, 1893–1894, *H. Hallier 3188* (holo BO! iso L); Sungai Betas Dalam, 29 Apr 2006, *A.P. Keim 757* (BO!); Bukit Siman, Camp 35, 30 Apr 2006, *A.P. Keim 764* (BO!); **Central Kalimantan**, Area Bukit Raya, Km 44, Sungai Wah, Kasongan, Sinamang Mentikay, 1 May 2006, *A.P. Keim 766* (BO!); **East Kalimantan**, Mount Kemoel, Km 47, 10 Oct 1925, *F.H. Endert 3875* (BO!); Nunukan Island, N of Tarakan, Nov 1953, *W. Meijer 2163* (BO!); **South Kalimantan**, Bandjarmasin-Martapoera, Km 14, 12 Oct 1939, *B. Polak 494* (BO!); **Moluccas**, Ambon, *Teysman s.n.* (holo BO! iso L); **West Java**, Banten, Gunung Tukung Gede Nature Reserve, Cikolelet, 02 Oct 2009, *T. Djarwaningsih 1499* (BO!).

3. *Freycinetia* cf. *tenuis* Solms (Fig. 6)

Slender climbing *pandan*, up to 40 m. *Leaves* small, short, lanceolate-elongate, c. 6 cm long, 0.5 cm wide, apex acuminate and with minute spines, spines only on terminal and basal parts of leaf; adaxial surface green, glabrous; abaxial surface pale green, glabrous; leaf sheath deep purplish red, apical part with minute spines; auricle tapered, small, deep purplish green to red.

Distribution. Sumatra and Borneo. In the Bukit Baka Bukit Raya National Park the species was only found at one site and appears to be rare.

Habitat. Lowland tropical rain forest. In Bukit Baka Bukit Raya, it is found in a rather open area close to a creek.

Vernacular name and uses. Not recorded.

Notes. Unfortunately the only specimen collected in this current study (*AK 769*) is a sterile one. Identification of this material as possibly belonging to *F. tenuis* is based on the habit, leaf dimensions, and colouration of auricles, which are in accordance with the protologue (Solms 1879; see also Warburg 1900), particularly the distinctive deep purplish red leaf sheath and tapered auricles. *Freycinetia tenuis* is the smallest member of the genus in Borneo. The species was recorded for Borneo by Stone (1970a) in Sabah, North Borneo; thus, as in the case of *F. sumatrana*, the presence of *F. tenuis* in Borneo strengthens the biogeographical link between Sumatra and Borneo (i.e., Sahulland).

Specimens examined: INDONESIA. **Central Kalimantan**, Kantor PT Sari Bumi Kusuma Timber, Katingan Hulu, Kota Waringin Timur, 1 May 2006, *A.P. Keim 769* (BO!); **South Kalimantan**, Bandjermasin to Martapoera, Km 14, 12 Oct 1939, *B. Polak 513* (A, BO! L).

Fig. 6. *Freycinetia* cf. *tenuis* Solms (*A.P. Keim 769*) showing the very slender habit and small lanceolate-elongate leaves; the overlapping leaf sheaths along the stem are a characteristic deep purplish red in live specimens, with tapered auricles. Photo: A.P. Keim, Rugayah & H. Rustiami.

Pandanus

1. ***Pandanus aristatus*** Martelli, Webbia 4 (1): 6 (1913). TYPE: *H. Hallier 2250* (holo BO! iso FI), Indonesia, Kalimantan (then Dutch Borneo), Sungai Djemala, Gunung Kelam, 1893–1894. (Fig. 7)

Pandanus andersonii H.St.John, Pacific Sci. 15(4): 576 (1961). TYPE: *J.A.R. Anderson s.n.* (holo SAR), Malaysia, Sarawak, Lawas, Kayangeran Forest Reserve, Nov 1960. PARATYPE: *J.A.R. Anderson S2815* (SAR), Malaysia, Sarawak, Loba Kabang Protected Forest, 16 May 1954.

Robust shrubby *pandan*, 2–3 m high. *Prop roots* absent. *Stem* very short (1.5–2 cm) or stemless. *Leaves* in a rosette of 20 or more, spirally arranged in 3 ranks (tristichous); each leaf lanceolate-elongate, 250–350 cm long, 4–10 cm wide, stiff, apex acute to acuminate, margin with obvious spines throughout the length; adaxial surface green, glabrous, main vein apparent, adaxial ventral pleats not observed or present; abaxial surface pale green, glabrous, main vein obvious, recurved spines obvious, very sharp; leaf sheath white to yellowish white. *Staminate inflorescence* terminal, creamy white, 107–115 cm long; rachis 44–66 cm long, with 8–10 rachillae; rachilla elongate, 28–30 cm long; peduncle 68–70 cm long, glabrous; bracts 13, each 10–140 cm long, persistent, boat shaped, pale brown. *Staminate flower* pale creamy yellow, odorous; stamens numerous. *Pistillate inflorescence* terminal, ascending; peduncle 10 cm long, diameter 2.5 cm, obtusely trigonous. *Infructescence* terminal, pendulous, 15–20 cm long, with a solitary cephalium or a spike consisting of 2 to 3 unequally sized cephalia; peduncle c. 8.5 cm. *Cephalium* elongate-ellipsoid or broadly ellipsoid to subglobose, obtusely trigonous, light to dark brown, 8.5–14 cm, c. 3 cm diameter, consists of numerous drupes. *Drupe* oblong-ellipsoid, 35–80 mm long, 6–7 mm wide, 5–6 mm thick, fusiform, 5–6 angled; pileus conical, 13–17 mm long, gradually narrowed into the style; style 5–7 mm long, subulate, arcuate, beaked, glabrous; stigma 4–5 mm long, appointed, needle-like and sharp.

Distribution. Borneo.

Habitat. Peat swamp forest, riversides and riverine forest. In villages close to the Bukit Baka Bukit Raya National Park, this species is cultivated. *Pandanus aristatus* is the most abundant species in the National Park and surrounding areas, particularly in the peat swamp forests.

Vernacular name. Kajak (Dayak, Belaban dialect).

Uses. Leaves used for baskets, mats, bags, hats, and handicrafts.

Notes. Previously *P. aristatus* was known only from the type (*H. Hallier 2250*), which is a staminate collection. As the classification of the Pandanaceae is basically based

Fig. 7. *Pandanus aristatus* Martelli. **A.** Robust-shrubby and stemless habit with large male inflorescence, beside the Nenga Pinoh-Sintang Highway, West Kalimantan. **B.** Staminate inflorescence at anthesis showing numerous minute, crowded, pale creamy yellow male flowers and layers of pale brown bracts; same venue as A. **C.** Within the Bukit Baka Bukit Raya National Park, *P. aristatus* is common along riversides. Photos: A.P. Keim & H. Rustiami.

on pistillate characters, the identity of *P. aristatus* was thus unresolved. Pistillate material is apparently rare, as even the present study has only succeeded in obtaining five staminate collections from various area and habitats within the National Park to the Nenga Pinoh-Sintang highway (Fig. 7), including the Gunung Kelam Ecopark (the type locality); these were from riversides to peat swamp forests or open areas. These findings not only increase the known distribution of the species, but also add new information on preferred habitats. A visit to the type location was also without success as individuals observed were not in flower or fruit. Nonetheless, the comparison between these five specimens and the holotype available at BO indicate that they undoubtedly belong to *P. aristatus*.

Apart from the lack of pistillate material in *P. aristatus* and staminate material in *P. andersonii*, no other significant morphological character could be used to differentiate *P. andersonii* from *P. aristatus*. Also, besides sharing the same habit as robust shrubby *pandan* with extremely short stems (less than 50 cm high); the two taxa also inhabit the same habitat, peat swamp forests. St. John (1961) described *P. andersonii* as the dominant species in peat swamp areas. Stone (1993) even stated that *P. andersonii* was a distinctive species of freshwater swamp forest, as is the case with *P. aristatus*. Now that the pistillate data for *P. aristatus* has become available; it is clear that *P. aristatus* belongs to subgenus *Acrostigma* and section *Acrostigma*. A specimen from South Kalimantan (*J. Dransfield & D. Saerudin 2102*) has been identified by the senior author as belonging to *P. aristatus*. *Pandanus aristatus* is regarded as one of the three main species in the peat swamps of Borneo, the other two being *P. atrocarpus* and *P. yvanii*.

Specimens examined: INDONESIA. **West Kalimantan**, Kampung Belaban, 1 May 2006, *A.P. Keim 768* (BO!); Km 35, Kampung Belaban, 3 May 2006, *A.P. Keim 776* (BO!); Nenga Pinoh-Sintang, Kampung Pandan, 5 May 2006, *A.P. Keim 778* (BO!); **Central Kalimantan**, Katingan Hulu, Sungai Sahaur, Km 54, 2 May 2006, *A.P. Keim 771* (BO!); *A.P. Keim 772* (BO!); **South Kalimantan**, Djaro Dam, Muara Uja, 11 Nov 1971, *J. Dransfield & D. Saerudin 2102* (BO! KLU, L).

2. *Pandanus discostigma* Martelli, Webbia 4 (1): 12 (1913). TYPE: *Jaheri 662* (holo BO!), Indonesia, Central-West Kalimantan, Maguc River, Nieuwenhuis Expeditie, 1896–1897. (Fig. 8 & 9)

Pandanus matthewsii Merrill, J. Str. Br. Roy. Asiat. Soc. 85: 153 (1922). TYPE: *Ramos 1321* (holo PNH† iso BO!), Malaysia, Sabah, Sandakan.

Slender clustered shrubby *pandan*, 0.5–1 m high. *Prop roots* very short, not obvious. *Stem* very short, not obvious, brown to reddish brown. *Leaves* in a rosette, spirally arranged in 3 ranks (tristichous); each lanceolate-elongate, c. 56 cm long, c. 1.5 cm wide, apex acuminate, margin with minute spines throughout the length; adaxial surface green, glabrous, adaxial ventral pleats not obvious; abaxial surface pale green,

Fig. 8. *Pandanus discostigma* Martelli. **A.** Slender clustered habit of plants beside the Betas Dalam River in the Bukit Baka Bukit Raya National Park, with other populations found submerged. **B.** Young solitary and terminal pale yellow cephalium. Photos: A.P. Keim, Rugayah & R. Asmarayani.

glabrous, recurved spines present; leaf sheath purplish red. *Inflorescence* terminal, solitary. *Cephalium* globose, c. 9 cm long, 11.5–16.5 cm in circumference, pale creamy yellow when young, turning brownish yellow when mature, cephalium consists of numerous creamy yellow drupes; style short; stigma depressed to form a disc-like structure, brown.

Distribution. Borneo.

Habitat. Riversides in lowland tropical rain forest. In the National Park, the species occurs sparsely along riversides (Fig. 8) and plants are sometimes submerged.

Vernacular name. Ries (Dayak, Belaban dialect).

Uses. Cephalium and leaf are used to cure (stop) hyperurination in children.

Notes. Prior to this, *P. discostigma* was only known from the type. (Martelli 1913; see also Stone 1993). Although the exact location of Maguc River remains unknown, the Nieuwenhuis expedition covered most of the central-western part of Kalimantan, including the numerous tributaries that run through Menikung and Melawi. Thus, it is possible that the locations where the collections were made during the present study were in the vicinity of the Maguc River.

Our study agrees with Stone that *P. matthewsii* is a synonym of *P. discostigma*, based on the unique disc-like stigma (Fig. 9) and also comparison with the two collections of *P. matthewsii* available at BO (*Endert 4904* and *B.C. Stone 6690*). *P. discostigma* is now considered a widespread species found along the rivers of lowland forests in Borneo.

Specimens examined: INDONESIA. **West Kalimantan**, Sungai Betas Dalam, Km 37, Menikung, Melawi, 28 Apr 2006, *A.P. Keim 751* (BO!); Bukit Siman, Sungai Ela, 30 Apr 2006, *A.P. Keim 765* (BO!); **Central Kalimantan**, Maguc River, Nieuwenhuis Expedition, 1896–1897, *Jaheri 662* (holo BO! iso L); Kuala Kuangan, Sei Sampit, 27 Feb 1982, *J.J. Afriastini 428* (BO!); **East Kalimantan**, West Koetai, Km 19, Poekoes Hill, 14 Nov 1925, *F.H. Endert 4904* (BO!) — MALAYSIA. **Sabah**, Sandakan, *Ramos 1321* (PNH† iso BO!); Leila FR, 17 Mar 1967, *B.C. Stone 6683* (BO!).

3. *Pandanus epiphyticus* Martelli, Nuov. Bull. Soc. Bot. Ital. 11: 304 (1904). TYPE: *Beccari s.n.* (holo FI), Malaysia, Sarawak, Mt. Mattang, near Kuching, Jun 1866. (Fig. 10)

Pandanus trigonus H.St.John, Pacific Sci. 19(1): 98, f. 207 (1965). TYPE: *H.N. Ridley s.n.* (holo K; iso SING), Malaysia, Sarawak, Bau. PARATYPE: *A.D.E. Elmer 21022* (BO! C, M, NY, PNH† SING), Malaysia, Sabah (then British North Borneo), Tawao, Oct 1922–Mar 1923.

Fig. 9. *Pandanus discostigma* Martelli has a fairly globose cephalium consisting of numerous drupes with distinctive disc-like stigmas that characterise this species, a character which supports the placement of *P. matthewsii* into its synonymy. Photo: A.P. Keim, Rugayah & R. Asmarayani.

Epiphytic *pandan*, c. 2 m high. *Leaves* in rosette, spirally arranged in 3 ranks (tristichous); each leaf lanceolate-elongate, 262–300 cm long, 9–10 cm wide, apex acuminate, margin with spines throughout the length; adaxial surface deep green, glabrous, adaxial ventral pleats not observed; abaxial surface pale green, glabrous, basal part with spines, recurved spines obvious; leaf sheath white and yellow. *Infructescence* terminal, 60–65 cm long, a spike consisting of 10 cephalia, cephalia not uniform in size, the most terminal one being the smallest; rachis c. 38 cm long, glabrous; peduncle 22–27 cm long, glabrous; bracts persistent. *Cephalium* elongate ellipsoidal, sausage-like, noticeably trigonous, yellowish white to dull greyish white, consisting of numerous compactly arranged drupes; style very short or sessile, not pointed; stigma short, not pointed, deep brown.

Distribution. Borneo, Malay Peninsula, and presumably also in Sumatra. Stone (1993) mentioned that the species used to be fairly frequently seen in Johor, Malay Peninsula before severe deforestration took place. One of the authors of this current study (APK) reported seeing *P. epiphyticus* in the peat swamp forest of Pelalawan in Riau, Sumatra in 2007, but no collection was made.

Fig. 10. *Pandanus epiphyticus* Martelli. An infructescence spike consisting of 10 elongate ellipsoid and trigonous, dull greyish cephalia. Photo: A.P. Keim & R. Asmarayani.

Habitat. This species is an epiphytic plant in lowland tropical rain forest, commonly found along gorges or riversides. In Bukit Baka Bukit Raya National Park, it is abundantly found in lowland forest, especially in the foot hills or close to rivers.

Vernacular name. Kajak (Dayak, Belaban dialect).

Uses. Leaves are used for thatching. Local people reported that the cephalium is eaten by orang utan and gibbons.

Notes. The presence of *P. epiphyticus* in Indonesian Borneo (Kalimantan) was reported by Stone (1993) based on a single collection, *Kostermans 9115* (BO! duplicate at L; see Stone 1993) from Nunukan, East Kalimantan. Nunukan is an island off the mainland East Kalimantan, so the present study confirms the presence of this species on the mainland.

Specimens examined: INDONESIA. **West Kalimantan**, Km 37, Sungai Betas Dalam, Menukung, Melawi, 28 Apr 2006, *A.P. Keim 747* (BO!); **East Kalimantan**, Nunukan, Northern part, 19 Dec 1953, *A. Kostermans 9115* (BO!) — MALAYSIA. **Sabah**, Tawao, Elphinstone Province, Oct 1922–Mar 1923, *A.D.E. Elmer 20490* (BO! PNH†); *A.D.E. Elmer 21022* (para BO! C, M, NY, PNH† SING).

4. *Pandanus pachyphyllus* Merrill, J. Str. Br. Roy. Asiat. Soc. 85: 154 (1922). TYPE: *Ramos 1541* (holo PNH† iso BO! A), Malaysia, Sabah, Sandakan. (Fig. 11 & 12)

Pandanus apicalis H.St.John, Pac. Sci. 22: 523, f. 276 (1968). TYPE: *Motley 1247* (holo K; iso BO! SING), Indonesia, Kalimantan (then Dutch Borneo), Banjarmasin, 1857–1858.

Robust shrubby *pandan*, 1–1.5 m high. *Prop roots* present, very short. *Stem* very short, not obvious. *Leaves* in a rosette, spirally arranged in 3 ranks (tristichous), 20–more leaves in a rosette; each leaf lanceolate-elongate, 205–206 cm long, c. 3.5 cm wide, apex acuminate, margin with obvious spines throughout the length; adaxial surface deep green, glabrous, adaxial ventral pleats present; abaxial surface pale green, glabrous, recurved spines present, obvious, very sharp. *Infructescence* terminal, solitary, c. 10 cm long; rachis c. 5 cm long, glabrous; peduncle c. 5 cm long, glabrous. *Cephalium* globose, yellowish green; style pointed, ascending; stigma pointed, sharp; in general appearance the cephalium superficially resembles the fruit of *durian* (*Durio zibethinus*, Malvaceae).

Distribution. Borneo.

Habitat. Foothills and gorges in lowland tropical rain forest. In Bukit Baka Bukit Raya National Park, the species is commonly found in gorges. Although abundant, most were not fruiting.

Fig. 11. *Pandanus pachyphyllus* Merrill: a robust shrubby pandan with a very short, almost invisible, stem, and a terminal infructescence with a globose cephalium. Photo: A.P. Keim, Rugayah & H. Rustiami.

Vernacular name. Selinsik (Dayak, Belaban dialect).

Uses. Leaves are used for mats.

Notes. The record of *P. pachyphyllus* in Kalimantan was only based on the type of *P. apicalis*, which was placed as a synonym of *P. pachyphyllus* by Stone (1978). Observations made on the types of *P. apicalis* and *P. pachyphyllus* at BO, and the collection made in this current study, indicate that there is no substantial difference. The distribution of this species could be more widespread in Borneo than previously thought.

Specimen examined: INDONESIA. **Central Kalimantan**, Km 44, Sungai Wah, Kota Waringin Timur, Kasongan, Sinamang Mentikay, 1 May 2006, *A.P. Keim 767* (BO!).

Fig. 12. *Pandanus pachyphyllus*: a terminal infructescence with extremely short peduncle and solitary yellowish green *durian*-like cephalium. This photo also shows the conspicuous spines all along the leaf margin. Photo: A.P. Keim, Rugayah & H. Rustiami.

5. ***Pandanus yvanii*** Solms, Linnaea 42: 20 (1878). TYPE: *Yvan s.n.* (holo Herb. Delessert), Malaysia, Malay Peninsula, Malacca. (Fig. 13–16)

Pandanus motleyanus Solms, Linnaea 42: 21 (1878). SYNTYPES: *Korthals s.n.* (L), Indonesia, Kalimantan (then Dutch Borneo); *Motley 1057* (K), Malaysia, North Borneo.

Pandanus ridleyi Martelli, Bull. Soc. Bot. Ital. (1904) 303. SYNTYPES: *Cantley s.n.* (K, SING), Malaysia, Sungai Ujong, Gunong Berumban; *Kunstler s.n.* (K, SING), Malaysia, Perak.

Pandanus brevifolius Martelli, Bull. Soc. Bot. Ital. (1914) 302. TYPE: *Beccari PB 273* (holo FI), Malaysia, Sarawak, Siul near Kuching.

Pandanus sigmoideus H.St.John ex B.C. Stone, Fed. Mus. J. 17: 124, f. 15 (1972). TYPE: *Brunig S12384* (holo L; iso K, SAR), Malaysia, Sarawak, Marudi, Baram, Lobok Pasir, Apr 1961.

Slender clustered tree *pandan*, 2–3 m high, commonly forming dense thickets. *Prop roots* short, 20 cm or less. *Stem* unbranched (*A.P. Keim 777*) or branched in the terminal part (*A.P. Keim 779*), slender, older bark dark purplish brown, spiny, diameter c. 1.5 cm. *Leaves* in a rosette, spirally arranged in 3 ranks (tristichous); each lanceolate-elongate, 40–45 cm long, 1–1.5 cm wide, apex acute to acuminate, margin with spines throughout the length; adaxial surface green, glabrous, adaxial ventral pleats absent; abaxial surface pale green, glabrous, recurved spines present, small, brown; leaf sheath yellowish green to yellow. *Infructescence* solitary, terminal, 17–20.5 cm long; bracts persistent, each 10–28 cm long, c. 2.5 cm wide, brown to deep brown. *Cephalium* ellipsoidal elongated, creamy yellow to dull creamy yellow or dull yellowish orange (*A.P. Keim 779*), 7.5–11 cm long, 13–14 cm in circumference; style ascending, needle-like, 2–2.5 mm long; stigma pointed, sharp.

Distribution. Malay Peninsula, Sumatra (including Bangka Island), and Borneo. Previously, *P. yvanii* was known as an endemic species of Malacca in the Malay Peninsula; thus we newly record the species for Sumatra, Bangka Island, and Borneo. In Bukit Baka Bukit Raya National Park, the species is hardly noticeable at higher altitudes but in the lowland open areas in full sun, and peat swamps in the vicinity of the National Park, the species is abundant (Fig. 13) and this is in accordance with Stone (1966).

Habitat. Peat swamps, where it usually forms dense thickets. *Pandanus yvanii* sometimes grows along riversides or in riverine forest.

Vernacular name. Rasau or *Rassau* (Dayak, Nanga Pinoh).

Uses. Not recorded.

Notes. Pandanus yvanii is a common species of peat swamp forests in the Malay Peninsula, Sumatra and Borneo (Stone 1993, as *P. motleyanus*). In a number of places in these areas, the species is widely known by the vernacular name *rassau*. This vernacular name was first recorded by Kurz (see Kurz ex Miquel 1866) for *P. helicopus* Kurz ex Miq.; however, a string of morphologically similar taxa have been published

Fig. 13. *Pandanus yvanii* Solms. **A.** Collector holding a severed stem in Nanga Pinoh. **B.** A dense thicket of stems. **C.** Stems with sharp nodules on the outer surface (and a characteristic deep reddish brown when fresh). **D.** A solitary, terminal elongate-ellipsoidal young cephalium (creamy yellow when fresh) with persistent deep brown bracts; notice the obvious dark spines along the leaf margin. Photos: A.P. Keim, Rugayah & H. Rustiami.

with almost all bearing "rassau" as one of their vernacular names. The classic case involves *P. helicopus*, *P. motleyanus*, and *P. yvanii*, which share a common habitat, peat swamps.

Unlike *P. helicopus*, the protologues of both *P. motleyanus* and *P. yvanii* (Solms 1878) describe fewer morphological details. The situation is worsened by the fact that instead of comparing *P. motleyanus* or *P. yvanii* with *P. helicopus*, Solms (1878) compared *P. motleyanus* only with *P. yvanii*, which was also published as a new species in the same publication, only a page earlier. The identity of *P. yvanii* as a species in its own right was first questioned by Hooker (1894), who described the morphological characters given in the protologue of *P. yvanii* as being worthless for the identification of a species of *Pandanus*. Apparently due to the limitted specimens available, Warburg (1900) distinguished *P. motleyanus* from *P. yvanii* based only on a minor morphological character, the colouration of the leaf spines (*P. motleyanus* has dark brown leaf spines; *P. yvanii*, light brown) and distribution (*P. motleyanus* in Borneo, *P. yvanii* in Malacca in the Malay Peninsula). Warburg numbered the two species one after the other (*P. yvanii* was 107, *P. motleyanus* was 108), thus suggesting their close affinity. Ridley (1925) followed Hooker in arguing that *P. yvanii* was too imperfectly described to identify the species and placed it as a synonym of Martelli's *P. ridleyi*.

Prior to the present study, *P. yvanii* was known only from a very few number of localities. BO has a specimen collected by Teijsmann in Muntok, Bangka Island (*Teijsmann s.n.*, BO! Fig. 14 & 15), which was named *P. yvanii* by Stone, but never published. This specimen possesses many morphological characters that match the protologue of *P. yvanii*, particularly the leaf and cephalium dimensions, and also the appearance of the style. We now have a firm record for the first time of its presence outside the type locality.

In contrast to Ridley (1925), this study places *P. ridleyi* in the synonymy of *P. yvanii*. Although there is a noticeable difference in the length of the cephalia, it is still within the range of *P. yvanii* and the synonymous *P. motleyanus*.

We place *P. sigmoideus* as a synonym of *P. yvanii*. St. John & Stone (1972) and Stone (1993) regarded *P. sigmoideus* as a distinct species from the then *P. motleyanus* based on the nature of leaf spines (reduced or obsolute, at most 1 mm long in *P. sigmoideus*, compared to developed, 1–2 mm long in *P. motleyanus*) and pollen surface (smooth in *P. sigmoideus*, minutely spinulose in *P. motleyanus*). We regard these two characters as less important and not discrete.

Martelli (1914) mentioned four distinctive characters of *P. brevifolius*: low shrub habit, brownish red stem, small leaves (hence the epithet "brevifolius"), and glabrous leaf margin. Observations made on specimens from Bukit Baka Bukit Raya and *Teijsmann s.n.* (BO! Fig. 14 & 15) indicate that those characters are also found in *P. yvanii*. Indeed, in the field *P. yvanii* can be seen as low shrubs with short brownish red stems, small narrowed glabrous leaves and subglobose cephalia; thus there is not sufficient reason to place *P. brevifolius* as a species on its own and it is regarded here as a synonym of *P. yvanii*.

Fig. 14. *Pandanus yvanii Solms* (*Teijsmann s.n.* "Muntok, Bangka", BO). This specimen shows two characters that match the protologue of *P. brevifolius*: small leaves without spines along the margin (see Martelli 1904). Photo: A.P. Keim.

Fig. 15. *Pandanus yvanii Solms* (*Teijsmann s.n.* "Muntok, Bangka", BO). This specimen shows two characters that match the protologue of *P. brevifolius* (see Martelli 1904): the deep reddish brown slender stem and small cephalium (apparently immature). Photo: A.P. Keim.

This present study does not agree with Stone (1993) in assigning *P. fruticosus* as a synonym of *P. motleyanus*. *Pandanus fruticosus* shares more similarities with *P. helicopus* in being a more robust pandan with longer (up to 5–10 mm long) drupes; whereas *P. motleyi* (or *P. yvanii*) is a more slender *pandan* with small (3 mm long) drupes. We regard *P. fruticosus* as a synonym of *P. helicopus*. Stone (1993), however, did recognise *P. yvanii* (then *P. motleyanus*) and *P. helicopus* as two distinct species.

Despite both being found in peat swamps, *P. yvanii* and *P. helicopus* occupy different ecological niches (Partomihardjo 2010 *pers. comm.*). *Pandanus yvanii* is commonly found forming dense thickets further inland in the peat swamps and has never been found on open riverbanks. On the contrary, *P. helicopus* is always found forming dense thickets along open riverbanks and streamsides in peat swamp areas and has never been found further in the forest. In other words, the two species are not fully cohabitant.

Also, the two species can almost instantly be identified in the field. *Pandanus yvanii* is a low shrub, possessing deep purplish brown stems, wide leaf scars, and bright yellow to yellowish green leafsheaths (Fig. 16). On the contrary, *P. helicopus* is larger, has pale brown stems, narrow leaf scars, and eye-catching bright orange-red leaf sheaths (Fig. 16).

Pandanus pumilus H.St.John shares many morphological characters and a habitat preference with *P. yvanii*; however, *P. pumilus* possesses a spike-like infructescence consisting of 4–5 cephalia (St. John 1961). *Pandanus yvanii*, so far as known, always has an infructescence with a solitary cephalium. The possibility of a variable pistillate inflorescence or infructescence structure needs to be further investigated. Until better data becomes available, we merely suggest that *P. pumilus* has a close affinity with *P. yvanii*.

Specimens examined: INDONESIA. **West Kalimantan**, Soengei Kelassar, 1893–1894, *H. Hallier 1549* (BO! L); West Koetei, 30 Nov 1925, *F.H. Endert 5413* (BO! L); Pontianak, Sei Raja, 12 Mar 1931, *Mondi 9* (BO! L); Pontianak, Kampoeng Mandor, 23 Dec 1931, *J.P. Schuitemaker 139* (BO! L); Mampawah, Mengkatja, 29 Sep 1948, *M. Enoh 399* (BO! K, L); Nanga Pinoh to Sintang, Kampung Pandan, 5 May 2006, *A.P. Keim 777* (BO!); *A.P. Keim 779* (BO!); *A.P. Keim 780* (BO!); **Central Kalimantan**, Sampit, 22 Aug 1940, *P. Buwalda 7647* (BO! L); Kapuas, Tewah, Desa Kasintu, 13 Oct 1999, *S. Riswan et al. TWH 025* (BO!); **East Kalimantan**, Nunukan Island, Tarakan, Samenggaris, Dec 1912, *Amdjah 1077* (BO!); Samarinda, Sungai Mukun, near Sango-Sango, 05 Aug 1952, *W. Meijer 1100* (BO!); Nunukan Island, N of Tarakan, SE of Kampong, 22 Nov 1953, *W. Meijer 2303* (A, BO! K, L, P, PNH, SING); Nov–Dec 1953, *W. Meijer 2308* (BO!); Nov–Dec 1953, *W. Meijer 2351* (BO!, L); 13 Dec 1953, *W. Meijer 2479* (BO!); West Kutei, Mount Palimasan near Tabang, on Belajan River, 09 Sep 1956, *A. Kostermans 12823* (BO!, L); **South Kalimantan**, Bandjarmasin-Martapoera, Km 19, 04 Oct 1939, *Polak 439* (BO!); Banjarmasin to Martapura, Km 22, 26 Jun 1974, *J. Dransfield & G. Hambali 4312* (BO!, L); 26 Jun 1974, *J. Dransfield & G. Hambali 4313* (BO!, L); **Sumatra**, Bangka Island, Muntok, *Teijsmann s.n.* (BO!).

Fig. 16. *Pandanus yvanii* (**A**) and *P. helicopus* (**B**) compared. *Pandanus yvanii* individuals are more slender compared to *P. helicopus* (photo taken in the Sebangau National Park, Central Kalimantan). Stems of *P. yvanii* are characteristically deep reddish brown with wider leaf scars; those of *P. helicopus* are bright reddish brown with distinctively narrow, dense and crowded leaf scars. The leaf sheath of *P. yvanii* is yellow or yellowish green, those in *P. helicopus* are strikingly reddish brown. Photos: A.P. Keim, Rugayah & H. Rustiami (A); E.A. Widjaja & M. Amir (B).

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A taxonomic study of the *Pandanus furcatus* and *P. tectorius* complexes (Pandanaceae) in Java

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ABSTRACT. Current taxonomic problems in *Pandanus* in Java include the interpretation of the *Pandanus furcatus* complex as well as the *P. tectorius* complex. A study of general morphological, stomatal and molecular characteristics (viz., the noncoding chloroplast intergenic spacer region *atp*B-*rbc*L) showed that *P. bantamensis* Koord., *P. pseudolais* Warb., and *P. scabrifolius* Martelli, previously considered synonyms of *P. furcatus*, and *P. tectorius* var. *littoralis* Martelli and *P. odoratissimus* L.f. are all distinct species.

Keywords. Anatomy, *atpB-rbcL*, Java, morphology, *Pandanus furcatus* complex, *Pandanus tectorius* complex

Introduction

The term species complex was used to describe a species aggregation sharing specific morphological and molecular features (Judd et al. 1999). Within such a complex, a complicated morphological overlap, without any discontinuities, has led to taxonomic difficulty (Pak and Kawano 1992). Although their taxonomic affinity may be difficult to determine, some form of taxonomic resolution is desirable.

According to Stone (1972), *Pandanus* Parkinson in Java contains many rather problematic species. He suggested that detailed studies were required to obtain a more refined taxonomic scheme. The main problem, as far as Javan plants are concerned, appears to be the status of taxa which are given as synonyms of *P. furcatus* Roxb. by Backer and Bakhuizen van den Brink f. (1968). These synonyms include *P. bantamensis* Koord., *P. oviger* Martelli, *P. pseudolais* Warb. and *P. scabrifolius* Martelli. Also, *P. odoratissimus* L.f was thought to be synonymous with *P. tectorius* var. *littoralis* Martelli. Stone (1972) made a short revision of Pandanaceae in Java based on herbarium specimens in the BO herbarium and living plants cultivated in the Hortus Bogoriensis, attempting to develop a more stable species concept for *Pandanus* *furcatus* Roxb. In Stone's opinion, Backer's species concept for *Pandanus furcatus* was far too comprehensive and required readjustment because distinct species were lumped with *Pandanus furcatus.* Stone regarded *P. bantamensis*, *P. oviger, P. pseudolais* and *P. scabrifolius* as four different species, whereas the status of *P. tectorius* var. *littoralis* and *P. odoratissimus* was still more or less in question. The circumscription of these taxa are reviewed in light of new studies based on material from our recent fieldwork in Java. A practical difficulty here was that almost all morphological characters and/or character states used for evaluating a species complex are only slightly differentiated from one another and usually show considerable overlap. Therefore the identification of taxa within a species complex usually required a combination of several characters. The aim of the study was to provide a taxonomic resolution of the *P. furcatus* complex and *P. tectorius* complex, based on general and stomatal morphology, and a molecular approach utilising the noncoding chloroplast intergenic spacer region *atpB-rbcL.*

Materials and methods

Studies of herbarium specimens were conducted in the Herbarium Bogoriense (BO), Herbarium of the Royal Botanical Gardens, Kew (K) and National Herbarium of the Netherlands, Leiden (L). Observations of living plants and stomatal studies were undertaken at BO, while the molecular data was analysed in the Van der Klauw Laboratory, Leiden.

Data on morphology were collected from herbarium specimens and fresh field collections. The procedure for treating morphological variation followed that described by Rifai (1976) and Vogel (1987). Measurements were taken from spirit-preserved material, dried herbarium specimens and living material. Floral parts were measured from spirit-preserved material, and material rehydrated (by boiling) from dried specimens.

Leaf stomatal characteristics were investigated by first fixing the leaves (a small part of the middle to basal area) in FAA. Paradermal sections were taken from the upper and lower surfaces of leaves, then stained with safranin 1% in water and mounted in glycerine (Johansen 1940).

Genomic DNA was extracted from leaf material dried in silica gel according to the protocol described by Doyle & Doyle (1987). Double-stranded DNA was directly amplified by PCR. Reaction volumes were 25 µl and contained 2.5 µl PCR buffer, 2.5 µl dNTPs, 1 µl each of the 5 mM primers, 0.3 µl *Taq Pol* and 12.7 µl ddH$_2$O. Approximately 5 µl genomic DNA was added to the PCR mixture. PCR was performed 3 min at 94°C for the activation of the polymerase, followed by 35 cycles of 49 sec at 94°C, 45 sec at 55°C, 2 min at 72°C, with a final extension period of 10 min at 72°C. The primers used in this study for *atpB-rbcL* intergenic spacers are (forward 5'-GAAGTAGTAGGATTGATTCTC- 3') and (reverse 5'-TACAGTTGTCCATGTACC AG-3'). The PCR product was checked on 1% agarose gel, and purified using a purification kit of Wizard SV Gel and PCR clean up system (PROMEGA) following the manufacturer's protocol prior to sequencing. The DNA concentration was measured with the nanodrop. Cycle sequencing was performed by Macrogen Korea. The sequences were edited using sequencher 4.6 and MEGA 3.0 (Kumar et al. 2004).

Results

Morphological characters of the Pandanus furcatus complex

For this study, we found only three of the four species recognised within the *P. furcatus* complex, i.e., *P. bantamensis*, *P. pseudolais* and *P. scabrifolius*. Several characters studied are compared in Table 1. Prickles on prop-roots did not appear to display consistent differentiation among taxa, although *P. scabrifolius* did not have prickles on the prop-roots. Leaf dimensions were highly variable. *Pandanus pseudolais* tended to have longer leaves, whereas the leaves of *P. scabrifolius* had a shorter range of length measurements. *Pandanus bantamensis* had intermediate leaf length. The number of drupes per cephalium of *P. pseudolais* was higher than in the other two taxa. *Pandanus scabrifolius* had longer drupes compared with the other two taxa.

Four other characters studied were leaf base colour, peduncle shapes, fruit shapes and style shapes, that appeared to be useful for discriminating among species (Table 1). *Pandanus bantamensis* and *P. pseudolais* had a reddish brown leaf base, and *P. scabrifolius* a yellowish white leaf base. The peduncle was stout and quite straight in *P. scabrifolius*, and curved in the other two taxa. *Pandanus scabrifolius* also had a broadly ellipsoid cephalium, compared to the narrower cephalia in the other two species; it also had comparatively shorter style bifurcations (divisions a third the style length or less) than in the other two species (divisions about half the style length).

Table 1. The *Pandanus furcatus* complex: some morphological features of the vegetative parts, peduncle, fruiting cephalium, drupes and style in the three taxa studied.

Character	*P. bantamensis*	*P. pseudolais*	*P. scabrifolius*
Leaf length (cm)	216–441	299.4–574.5	204–372
Prickles on prop-root	present, prickles in rows	present, prickles in rows	smooth
Number of drupes	475–795	724–1053	473–483
Drupe length (cm)	2.7–4.5	2.6–4.5	4.8–5.2
Leaf base colour	Reddish brown	Reddish brown	Yellowish white
Peduncle shape	Slightly curved at the base	Strongly curved at the base	Straight
Cephalium shape	Narrow-ellipsoid	Narrow-ellipsoid	Broad-ellipsoid
Style bifurcation	Divisions about half the style length	Divisions about half the style length	Divisions a third of the style length or less

Morphological characters of the Pandanus tectorius complex

Leaf dimension, leaf shape, cephalium size and shape, and the number of phalanges per cephalium did not have any consistent differences between the taxa analysed (Table 2). However, *P. tectarius* var. *littoralis* had leaf apex prickles only on one surface (*P. odoratissimus* has prickles on both surfaces of the leaf apex); and carpel apices that were essentially fused, withour any deep grooves between carpels (*P. odoratissimus* had carpel apices that were free, leaving deep grooves between carpels) (Table 2).

Table 2. The *Pandanus tectorius* complex: morphological characteristics of *P. tectorius* var. *littoralis* and *P. odoratissimus*.

Characters	*P. tectorius* var. *littoralis*	*P. odoratissimus*
Leaf length (cm)	112–199	98–126
Leaf shape	ligulate or sword-shaped	ligulate or sword-shaped
Cephalium size (cm)	26 × 25	22 × 25
Cephalium shape	broad-ellipsoid	broad-ellipsoid
Number of phalanges	79–83	73–83
Prickles on leaf apex	only on one side of leaf, the other side smooth	on both sides of leaf
Carpel apices	fused, without deep grooves between carpels	not fused, with deep grooves between carpels

Stomatal characters

Five classes of stomatal features (Tomlinson 1965, Kam 1971) are known in *Pandanus*, depending on the number of papillae that develops on the subsidiary and neighbouring cells. In the *Pandanus furcatus* complex, *P. bantamensis*, *P. pseudolais* and *P. scabrifolius* had stomatal Class 2 (papillae only occurring on lateral subsidiary cells), Class 1 (papillae absent: unspecialized stomata) and Class 3 (papillae in both terminal and lateral subsidiary cells) of Tomlinson (1965), respectively. Within the *Pandanus tectorius* complex, *P. tectorius* var. *littoralis* had stomatal Class 4 (papillae occurring in both lateral subsidiary and neighbouring epidermal cells) and *P. odoratissimus* had stomatal Class 2 (papillae only occurring on lateral subsidiary cells).

Molecular characteristics

Although the small number of taxa investigated would not be expected to yield any meaningful phylogenetic analysis, the *atpB-rbcL* intergenic spacer region provided potential markers for distinguishing the different species in both of the complexes.

There were 29 polymorphic sites in this region for the three species of the *Pandanus furcatus* complex investigated (Table 3), of which 19 sites were different between *P. bantamensis* and *P. pseudolais*, 24 sites were different between *P. pseudolais* and *P. scabrifolius*, and 21 sites were different between *P. bantamensis* and *P. scabrifolius*. Likewise, there were 71 polymorphic sites in this region for the two species of the *Pandanus tectorius* complex investigated (Table 4).

Table 3. The *Pandanus furcatus* complex: polymorphic sites in the *atpB-rbcL* intergenic spacer region.

Species	Nucleotide at polymorphic site at indicated position																		
	4	6	16	17	18	121	123	149	150	166	167	168	249	271	272	273	292	293	296
P. bantamensis	A	G	A	A	A	C	C	G	A	A	G	T	T	A	A	T	T	T	A
P. pseudolais	T	T	A	C	C	A	T	A	A	A	A	T	A	G	G	A	A	T	A
P. scabrifolius	T	G	C	C	T	T	C	A	G	G	T	G	T	G	A	G	T	A	T

Species	Nucleotide at polymorphic site at indicated position									
	297	446	447	448	520	521	522	550	551	552
P. bantamensis	G	T	A	G	A	C	C	T	C	A
P. pseudolais	T	G	G	G	A	T	A	T	T	A
P. scabrifolius	A	T	A	A	T	A	C	A	T	C

Discussion

Pandanus furcatus complex

The species recognised within the *Pandanus furcatus* complex shared some morphological similarities, but could be distinguished by leaf base colour, peduncle shape, fruit shape, style shape, and stomatal characteristics. A number of sites in the *atpB-rbcL* intergenic spacer region were also polymorphic for these species. We conclude that *Pandanus bantamensis*, *Pandanus pseudolais* and *Pandanus scabrifolius* are three distinct species. Our study thus corroborates the conclusions of Stone (1972).

Table 4. The *Pandanus tectorius* complex: polymorphic sites in the *atpB-rbcL* intergenic spacer region.

Species	Nucleotide at polymorphic site at indicated position															
	31	32	33	61	62	63	85	86	87	115	117	119	120	199	200	201
P. tectorius var. *littoralis*	A	G	T	T	C	T	T	A	A	G	T	T	C	C	T	C
P. odoratissimus	G	T	A	G	A	C	G	T	T	A	A	A	G	T	G	A

Species	Nucleotide at polymorphic site at indicated position															
	204	229	231	232	233	241	242	260	269	334	335	336	380	405	438	441
P. tectorius var. *littoralis*	T	A	G	G	A	A	T	T	T	C	A	T	A	G	C	C
P. odoratissimus	A	G	T	T	C	T	A	A	A	T	T	G	T	A	A	C

Species	Nucleotide at polymorphic site at indicated position															
	464	465	476	477	507	520	521	571	573	578	579	586	589	590	591	608
P. tectorius var. *littoralis*	A	G	A	A	G	T	C	A	A	A	C	G	A	A	T	T
P. odoratissimus	G	A	T	T	C	A	A	T	T	G	G	C	C	C	A	G

Species	Nucleotide at polymorphic site at indicated position															
	609	613	614	623	739	740	748	770	771	774	775	789	809	810	856	857
P. tectorius var. *littoralis*	G	A	C	T	C	A	T	C	A	A	C	T	G	T	A	G
P. odoratissimus	A	T	T	C	A	G	G	A	C	G	A	G	A	A	T	A

Species	Nucleotide at polymorphic site at indicated position						
	858	895	896	897	901	902	903
P. tectorius var. *littoralis*	A	A	A	A	G	G	A
P. odoratissimus	C	G	T	C	T	C	C

Key to three species of the *Pandanus furcatus* complex

1a. Leaf base reddish brown; cephalium narrowly ellipsoid (the length almost 3 times the width); style bifurcations about half the style length 2
1b. Leaf base yellowish white; cephalium broadly ellipsoid (the length at most twice the width); style bifurcations a third of the style length or less ...... *P. scabrifolius*

2a. Peduncle slightly curved at the base; cephalium with 475–795 drupes; stomata type "Class 2", with papillae on lateral subsidiary cells .... *P. bantamensis*
2b. Peduncle strongly curved at the base; cephalium with 724–1053 drupes; stomata type "Class 1", without papillae .... *P. pseudolais*

Pandanus tectorius complex

Although *Pandanus tectorius* var. *littoralis* and *P. odoratissimus* are very closely related (Stone 1994). Stone (1967) had proposed delimiting *P. odoratissimus* by just two characters: fleshy shoulders on phalanges and large white spines on the leaves. In our study, *P. odoratissimus* was found to have large white spines on the leaves as described, but the same could also be found in *P. tectorius* var. *littoralis*. *Pandanus odoratissimus* also does not have fleshy shoulders on the phalanges. Our observations tally with those of Stone (1979) who stated that *P. odoratissimus* has large white spines, but does not have fleshy shoulders. In this study, we have found several contrasting morphological characters that could be useful for distinguishing these two species. *Pandanus tectorius* var. *littoralis* has a leaf apex that is prickly on only one side of the leaf and fused carpel apices without any significant grooves in between; whereas *P. odoratissimus* has a leaf apex that is prickly on both sides of the leaf and free carpel tips separated by deep grooves in between. As many as 71 sites in the *atpB-rbcL* intergenic spacer region were also found to be polymorphic between these two taxa. We therefore accept these two taxa as specifically distinct.

Key distinguishing *Pandanus tectorius* and *P. odoratissimus*

1a. Leaf apex prickly only one one side; stomata with papillae on neighbouring epidermal and subsidiary cells; carpel apices fused and without any significant grooves in between .... *P. tectorius* var. *littoralis*
1b. Leaf apex prickly on both sides; stomata with papillae on lateral subsidiary cells only; carpel apices free and separated by deep grooves in between ....
.... *P. odoratissimus*

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Bothriochloa (Poaceae: Andropogoneae) in Malesia

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ABSTRACT. In Malesia there are four species of *Bothriochloa* (Poaceae: Andropogoneae). *Andropogon modesta* is lectotypified.

Keywords. Andropogoneae, *Bothriochloa*, Malesia, Poaceae

Introduction

Bothriochloa Kuntze is a small genus of grasses with about 35 subtropical and tropical species (Clayton et al., 2008). It belongs to the Andropogoneae, a subtribe that is especially developed in the tropics. The species are usually found in areas with a pronounced dry season, where they may become vegetation forming. There is no recent overall revision, only some local accounts, e.g., Deshpande (1984) for India, Vega (2000) for South America, Neamsuvan et al. (2009) for Thailand, and Sumadijaya & Veldkamp (2009) for Malesia.

The generic delimitation is problematic, as *B. bladhii* (Retz.) S.T. Blake, better known as *B. intermedia* (R.Br.) A.Camus or *B. glabra* (Roxb.) A.Camus, is a most curious species (see e.g., Wet & Harlan 1970). In general, the plants are hexaploid and cleistogamous, but occasionally some are outbreeding. The off-spring then is diploid, tetraploid and hexaploid and can hybridise with species with the same ploidy level, not only of *Bothriochloa*, but also with some of *Capillipedium* Stapf and *Dichanthium* Willemet. Thus it is able to transfer genetic information from one genus to another. The F1 of these is cleistogamous again, and so within its area of distribution from Africa to Australia and the Pacific there are a great number of local clonal forms, differing more or less, and causing the description of numerous taxa in all three of these genera. The synonymy is therefore bewildering.

Some have advocated to join the genera into one, the oldest name being *Dichanthium* for it, but then immediately recognise infrageneric taxa in it, one step down, with no knowledge gained (Wet & Harlan, 1968). It may be noted that intergeneric hybrids in grasses are just as common as in orchids, so hybridisation is no argument to join genera.

The diagnostic characters for the taxa are as follows: *Bothriochloa* with spikes in a panicle or subdigitate, partial peduncles not capillary, racemes with more than 10, very slender joints, the pedicels and joints with a longitudinal, translucent, resinous channel. *Capillipedium* has panicles with capillary branches, racemes with up to 9 joints, the pedicels and joints have resinous channels. *Dichanthium* has inflorescences similar to those of *Bothriochloa*, but the pedicels and joints have no resinous channel.

Distribution

Note that *B. bladhii* is the most widespread species which locally may become dominant, yet as far as herbarium records are concerned it is very rare in Borneo and apparently introduced in New Guinea. Only three Bornean specimens were seen in L and SING. Moreover, there is only single specimen collected from Buru island, in the Moluccas. These facts give these areas a higher priority for collection in the future.

Interesting is the disjunct distribution of *B. pertusa*. It occurs from Africa [as *B. insculpta* (Hochst. ex A.Rich.) A.Camus] to Burma and then in Java, Madura, and the Lesser Sunda Islands (Flores, Sawu, Sumba, Sumbawa, Timor). Said to have been introduced, but already in 1858 it was collected by Zollinger in Madura. It may well be an Ice age relictual distribution. This is a pattern that is often seen in species that need a more or less seasonal climate with pronounced dry periods. They follow the former drought tracks from Burma over the Sunda platform, and from Taiwan through the Philippines to Australia during the last Ice Age, when the sea was perhaps 120 m lower than today.

A surprising result of our study was that *B. ewartianus* (Domin) C.E.Hubb. reported in the herbarium and literature for the Lesser Sunda Isl. (Sumbawa, Timor), and Papua New Guinea (Central, Madang) could not be distinguished from *B. ischaemum* (L.) Keng. For its wide distribution in Australia see the map in Mallett & Orchard (2002). For that in Eurasia see Conert (1979).

Fig. 1. Distribution of *Bothriochloa* Kuntze in Malesia. Range marked with dots is used for *B. bladhii*, marked with crosses for *B. ischaemum*, and marked with dashes for *B. modesta*; blackened areas indicate *B. pertusa*.

The species are easy to distinguish. Important characters are the relative lengths of the main axis of the inflorescences and of the racemes: main axis longer or shorter than the lowermost racemes; also whether the lowermost racemes are whorled, or fascicled, or solitary; whether there are "pits" on the lower glume. It is not clear what the function of the latter is: it has been suggested that they would be extra-floral nectaries.

Key to the Malesian species

1a. Axis of the panicle much longer than the lowermost branches 2
1b. Axis of the panicle much shorter than the branches 3

2a. Axis of the panicle 10–20 cm long, possibly shorter in under-developed specimens. Racemes whorled, the lowermost often branched, with 8–many joints. Widespread .... *B. bladhii*
2b. Axis of the panicle 4–8 cm long. Racemes solitary, simple, with 3–6 joints. (E Java, Bawean, Madura, Bali) .... *B. modesta*

3a. Nodes usually glabrous. Blades usually glabrous. Upper glume setulose. (Lesser Sunda Isles, Papua New Guinea) .... *B. ischaemum*
3b. Nodes bearded. Blade usually hairy. Upper glume slightly rough. (Lower glume of sessile spikelet 1–3-pitted.) (Java, Madura, Lesser Sunda Isles) .... *B. pertusa*

LECTOTYPIFICATION: *Andropogon modesta* Backer, the basionym of *Bothriochloa modesta* (Backer) Backer & Henrard is lectotypified here with *Beumée 2672* (lecto BO; isolecto L, PNH†).

An index to Malesian specimens identified as the various species of *Bothriochloa* is given at the end of this account.

Excluded species

A single collection of *Bothriochloa saccharoides* (Sw.) Rydb. from an experimental garden in Manila was seen in L, with two other collections from that garden (without exact date and year) in BO. Therefore its presence is excluded from Malesia. *Bothriochloa kwashotensis* (Hayata) Ohwi and *B. parviflora* (R.Br.) Ohwi var. *mutispicula* Ohwi belong to *Capillipedium*.

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Appendix A. Index to the specimens.

bla = *Bothriochloa bladhii* (Retz.) S.T. Blake
isc = *Bothriochloa ischaemum* (L.) Keng
mod = *Bothriochloa modesta* (Backer) Backer & Henrard
per = *Bothriochloa pertusa* (L.) A. Camus

Afriastini 1664 (BO): bla; *1808* (BO): bla; *Alston 15312* (BO): bla; *Alvarez & Fernando 4195* (BO): bla; *Arendsen Hein 22* (BO): isc; *Arsin s.n.* (BO): bla; *Ass. Resident Timor s.n.* (BO): bla;

Backer Jul 1918 (L): bla; *134* (BO): bla; *6424* (BO): bla; *6630* (BO): bla; *6883* (BO): bla; *6986* (BO): bla; *9542* (BO): bla; *12950* (BO, L): bla; *13375* (BO, L): bla; *13405* (BO): per;

Backer 13496 (BO): bla; *13887* (BO): bla; *18089* (BO, L): bla; *20316* (BO): per; *20342* (BO): bla; *20342* (L): per; *20929* (BO): per; *21145* (BO): mod; *22807* (BO): bla; *23512* (BO, L): bla; *24184* (BO): isc; *24186-bis* (BO, L): mod; *24291* (BO): mod; *24321* (BO): per; *24402* (BO, L): bla; *24485* (BO): bla; *24531* (BO): bla; *24613* (BO): per; *24882* (BO, L): mod; *26407* (BO, L): bla; *26558* (BO): bla; *27055* (BO, L): bla; *27735* (BO): bla; *27987* (BO): bla; *28342* (L): per; *28530* (BO): bla; *28770* (BO): bla; *28996* (BO): bla; *29513* (BO): bla; *29670* (BO): bla; *30035* (BO): per; *30054* (BO): mod; *30409* (BO): isc; *30746* (BO): mod; *33579* (BO, L): bla; *33685* (BO): per; *36018* (BO): per; *36019* (L): per; *36096* (L): bla; *36217* (BO, L): mod; *36925* (BO): per; *37558* (L): per; *Bakhuizen* *van den Brink 4877* (BO, L): bla; *Brink 6755* (BO, L): per; *Balansa 1 Dec 1886* (L): per; *Beumée A 674* (BO): per; A *788* (BO): bla; *1013* (BO): mod; *1042* (BO, L): mod; *1498* (BO): bla; *2672* (BO, L): mod; 5396 (BO): bla; *5506* (BO): per; *Bloembergen 3207* (BO, L): bla; *3296* (BO, L): bla; *3320* (BO, L): bla; *Bouman 4* (L): bla; *Brown 8* (SING): bla; *BS 4858* (*Ramos*): (BO): bla; *6734 (Merrill)* (SING): bla; *30072 (Fénix):* (BO): bla; *84951 (Ramos & Edaño)* (SING): bla; *Bünnemeijer 1284* (BO, L): bla; *6001* (B), L, SING: bla; *3338* (BO, L): mod; *3812* (BO): bla; *8011* (BO, L): bla;

Carr 11329 (L, SING): bla; *CHB* (BO): bla; *Cinatti 38* (L): bla; *44* (L): bla; *46* (L): isc; *98* (L): per; *Classon K 43* (BO): mod; *Clemens 18198* (SING): bla; *Cuming 1400* (CGE, G, GOET, K, L, P,W): bla;

De Voogd 2443 (BO): bla; *2503* (BO): mod; *2530* (BO): bla; *De Wilde 22 Jun 1946* (L): bla;

De Wit 4114 (L): bla; *Docters van Leeuwen 19 Mar 1911* (L): per; *Dorgelo 3012* (L): per; *3021* (L): per;

Edeling 141 (BO): per; *Elbert 2885* (L): bla; *Elmer 12024* (BO): bla;

Fukuoka & Sukasdi J-1583 (BO): bla;

Gezagh. Sawoe 2 (BO): bla; *4* (BO): per; *Gouv. Veearts 4* (BO): per; *18* (L): per;

Gouvern. Veearts Soembawa B. (BO): bla; *Gouvern. Veearts te Watampone* (BO): bla; *Gutterink 3165* (BO): bla;

Hallier M 39 (BO): per; *M 41* (BO): per; *Henty 221* (L): mod; *Hoekstra 19* (BO, L): per; *Höft 2793* (L): bla; *3061* (L): bla; *3072* (L): bla; *Holttum 26 Oct 1946* (SING): bla;

Jaag 1200 (L): bla; *1395* (L): bla; *852* (L): bla; *Javasuikerindustrie 92* (BO): bla;

Kjellberg 3008 (BO): bla; *3704* (BO): bla; *Knaap 15* (BO): bla; *Kooy 660* (L): per; *688* (L): isc; *Kuswata 180* (BO): bla;

Lambinon 87/134 (L): bla; *Leefmans 94* (BO): per; *Lörzing 3732* (BO): bla; *5811* (BO): bla; *8069* (BO): bla; *8811* (BO): bla; *9033* (BO): bla; *9102* (BO, L): bla; *11010* (BO): bla; *11101* (BO): bla; *12885* (BO): bla;

Malvins 31 Jan 1886 (SING): bla; *Mehra 4* (BO): bla; *6* (BO): bla; *11* (BO): bla; *51* (BO): bla; *84* (BO): bla; *91* (BO): bla; *111* (BO): bla; *Mehra & Dadi Supriadi 1173* (BO): bla; *Metzner 90* (L): per; *Monod de Froideville 995* (BO, L): bla; *1028* (BO): bla; *1218* (BO): bla; *1243* (BO): per; *1376* (BO): per; *1444* (BO, L): bla; *1498* (BO, L): bla; *1515* (BO): bla; *1515a* (BO): bla; *1598* (BO, L): bla; *1621* (L): per; *1721 c* (BO): per; *1760* (BO): bla; *1818* (BO, L): bla; *1882* (BO): bla; *1884* (BO): bla; *1886* (BO): bla; *1893* (BO): bla; *1982* (BO, L): per; *1996* (BO, L): per; *1999* (BO): per; *2029* (BO): per; *2041* (BO): isc;

NGF 20987 (Henty) (L): bla; *22058* (*Gillison)* (L): bla; *39411 (Streimann & Kairo)* (BO): bla *49815* (*Henty & Katik)* (L): bla;

PNH 11401 (Farinas & Abordo) (L): isc; *17024 (Sulit)* (L): bla; *19065 (Conklin)* (L): bla; *20464 (Mendoza)* (L): bla; *82029 (Mendoza)* (L): bla; *Posthumus 2652* (BO): bla; *Proppe 22* (BO): bla; *23* (BO): bla; *33* (BO): per; *Pullen 3142* (L): isc; *6748* (L): bla;

Ramos 1842 (BO, SING): bla; *Reid May 1956* (SING): bla; *Ridley 14* (SING): bla; *11689* (SING): bla; *14844* (SING): bla;

Saakov 45 (BO): bla; *SAN 151251 (Laegaard et al.)* (L): bla; *151306 (Laegaard et al.)* (L): bla; *Santos J.V. 4607* (L): bla; *5095* (L): bla; *5104* (L): isc; *5240* (L): bla; *5826* (L): bla; *6089* (L): bla; *6280* (L): bla; *6365* (L): bla; *6613* (L): bla; *6763* (L): bla; *6883* (L): bla; *6906* (L): bla; *6950* (L): bla; *7313* (L): bla; *7323* (L): bla; *7364* (L): bla; *7387* (L): bla; *7422* (L): bla; *7426* (L): bla; *7578* (L): bla; *7587* (L): bla; *7648* (L): bla; *7718* (L): bla; *7815* (L): bla; *8116* (L): bla; *8253* (L): bla; *Schmutz 4969* (L): bla; *5047* (L): bla; *5933* (L): bla; *SF 7284 (Nur)* (SING): bla; *7771 (Ridley)* (SING): bla; *13301 (Burkill & Haniff)* (SING): bla; *22899 (Henderson)* (SING): bla; *Simon 4228* (L): per; *Sinclair 8879* (SING): bla; *Siwon 1026* (L): bla; *Sohns 4 (*BO): bla; *10* (BO): per; *18* (BO): bla; *Sumadijaya & Fanani 5* (BO): bla; *Sunarti & Hamzah PTU 34* (BO): bla;

Van Balgooy 5094 (BO, L): bla; *Van Borssum Waalkes 3157* (BO): bla; *Van der Meer & De Hoed 2099* (L): per; *Van Harreveld s.n.* (BO): per; *Van Leeuwen JEF 6* (L): bla; *TSIOF 2* (L): bla; *Van Ooststroom* 12645 (L): per; *Van Slooten 2065* (BO): per; *Van Steenis 6669* (BO): bla; *7514a* (BO, L): bla; *7763* (BO): mod; *11229* (BO): bla; *17(8)73 (BO)*: per; *17450* (BO): per; *17450* (mixed with *Zoysia matrella*) (L): per; *17473* (L): per; *17978* (L): per; *18062* (BO, L): bla; *18084* (BO, L): bla; *18476* (L): bla; *Veearts Sibolga 20* (BO): bla; *Veeartsenijk. Dienst 40* (BO): bla; *Veldkamp 6955* (L): mod; *Veldkamp 7165* (BO, L): bla; *8905* (BO, L): bla; *8961* (BO, L): bla; *Verheijen 3148 (*L): per; *5277* (L): bla; *Volkens 196* (SING): bla;

Walsh 13 (BO): bla; *42* (BO): bla; *Widjaja 4690* (BO): bla; *Widjaja & Hamzah 2950* (BO): bla; *Wisse 429* (BO): isc; *683* (BO): isc;

Yakob 6 (SING): bla;

Zollinger 3960 (Madura, 6 Jun 1858!) (L): per.

Saurauia (Actinidiaceae) of New Guinea: current status, future plans

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ABSTRACT. *Saurauia*, with approximately 300 species, is the largest of three genera within the family Actinidiaceae and is found in the tropical and sub-tropical regions of Asia, Central and South America. The family placement of the genus has changed several times, at times being placed in Ternstroemiaceae, Dilleniaceae and its own family, Saurauiaceae. The island of New Guinea may be a centre of diversity for *Saurauia* in South East Asia with more than 50 species. No comprehensive treatment of New Guinean *Saurauia* has been attempted since the work of Diels in 1922, despite complaints by later researchers that this publication is out of date and the subdivisions of the genus proposed therein are unsatisfactory. A full account of the family, including *Saurauia*, has yet to be covered in Flora Malesiana. This paper presents an introduction to the genus *Saurauia* in New Guinea and communicates plans for future research.

Keywords. Actinidiaceae, New Guinea, *Saurauia*

The family Actinidiaceae

The family Actinidiaceae Gilg & Werdermann contains c. 355 species within three genera—*Actinidia* Lindl. (which includes the kiwi-fruit, c. 30 species), *Saurauia* Willd. (c. 300 species) and *Clematoclethra* (Franch.) Maxim. (c. 25 species). The family occurs in tropical and subtropical Central America, South America and South East Asia and also in temperate Asia and northern Australia (Heywood 2007). According to the Angiosperm Phylogeny Group (APG) 3 (Stevens 2001 onwards), Actinidiaceae sits in the order Ericales as a sister group to the families Roridulaceae and Sarraceniaceae.

Actinidiaceae is a family of trees, shrubs and woody lianas with alternate or spiral, simple leaves with entire or serrate margins and no stipules. Inflorescences are axillary, with few to many unisexual or hermaphroditic flowers with free or fused petals, 10 to many stamens which may be fused to the base of the petals and a superior ovary, usually with three to five carpels (Heywood 2007). Flowers are usually pentamerous but exceptions occur. In pentamerous flowers the aestivation is quincunical (Dressler & Bayer 2004). Flowers are often white but can also be pink, red or yellowish brown. The fruit is a berry or (often in *Saurauia*) a capsule, usually containing many small seeds. Raphides occur in many plant parts (Dressler & Bayer 2004). Several species (of mainly *Actinidia*) are cultivated world-wide for their edible fruit and ornamental value.

The genus *Saurauia*

Saurauia, by far the largest genus in Actinidiaceae, occurs from Mexico southwards to Chile in the New World and then in the Old World from China to New Guinea (with one species in Queensland, northern Australia). They are conspicuously absent from Brazil and Africa. There are c. 60 species across Central and South America (Hunter 1966, Soejarto 1980), the remainder being found in the Old World.

Saurauia is a genus of small to medium trees and shrubs (sometimes scrambling). A prominent feature of many species of *Saurauia* is the distinctive indumentum of (often stiff) hairs and scales that cover many plant parts. In dried herbarium specimens, the indumentum is often chaffy and tan-coloured, making it easy to spot with a ×10 hand-lens, and sometimes with the naked eye. The flowers of *Saurauia* may be subtended by a bract and two bracteoles (Dickison 1972). Sepals are connate at the very base, filaments are adnate to petals at the base; filament bases may be connate, forming a ring. Anther dehiscence is via poricidal slits.

Saurauia was first described by Carl Ludwig von Willdenow in 1801 and placed by him in the family Tiliaceae (Willdenow 1801). Two different spellings were used in this original publication—*Sauraüa* on the description of the illustration plate and *Sauraуja* in the main body of text—most likely due to a printing error (Hoogland 1977). Both were used for over 170 years until Hoogland's 1977 proposal, that *Saurauia* be conserved over *Saurauja*, was accepted.

Between Willdenow's 1801 publication and the present day *Saurauia* has been assigned by different authors to a number of different families—most commonly Ternstroemiaceae (now Pentaphylacaceae), Dilleniaceae and Saurauiaceae (Fig. 1). In 1972 Dickison provided evidence based on detailed studies of floral morphology and anatomy that *Saurauia* belonged in the family Actinidiaceae.

Saurauia in South East Asia and current status in New Guinea

Saurauia has yet to be treated for the Flora Malesiana series (*Actinidia* is the only genus in the family Actinidiaceae to have been covered so far; Steenis 1950). A revision of the Peninsular Malaysia taxa is currently in progress (Rafidah Rahman, pers. comm.) which will be the first for the Flora Malesiana region since Diels's (now outdated) treatment of the New Guinea taxa in 1922. Diels's classification, looking only at New Guinea species, divided the genus into 10 sections: *Uniflorae, Ramiflorae, Calyptratae, Squamulosae, Setosae, Armatae, Obtectae, Rufae* (also inconsistently referred to in the manuscript as *Tomentosae* by Diels), *Bibracteatae* and *Obvallatae*. The sections are divided mainly on inflorescence architecture, bract characters, and leaf, bract and sepal indumentum.

Gilg & Werdermann (1925) later adapted Diels's system to encompass other Old World species (no extra New Guinean taxa were added) and modified it by sinking seven of Diels's 10 sections into one, thus dividing the genus into four sections: *Uniflorae, Ramiflorae, Calyptratae* and *Pleianthae*. The seven sections of Diels sunk into *Pleianthae* were retained as series.

These systems are now desperately outdated, as many more New Guinean species have been published (e.g., Diels 1929, Smith 1941, Kanehira & Hatusima 1943, Royen 1982, Takeuchi 2008) and authors have experienced difficulties in fitting new taxa into the generic framework laid down in the Diels (1922) and Gilg & Werdermann (1925) papers. Burtt (1936) noted that under Gilg & Werdermann's system, several closely related Old World species fell into different sections, leading him to believe that the classification was largely artificial. The same has been noted specifically in New Guinea taxa, in *Saurauia trugul* P.Royen, for example. Royen (1982) noted that the pubescence of the bracts and sepals placed the species in series *Bibracteatae*, but the species showed a closer affinity to *Obvallatae*. More recent publications (e.g., Takeuchi 2008) continue to complain about this lack of clarity. Diels, Gilg and Werdermann were however aware of the limitations of their work, with Diels (1922) noting that "the series suggested are intended only as a preliminary grouping" and Gilg & Werdermann (1925) stating: "we believe that future monographic work will change and improve the groupings".

A search of Index Kewensis records, via the International Plant Names Index (2010) reveals that c. 100 taxon names have been published for New Guinea. The first two New Guinea taxa were published by Miquel in 1869. During the 20 years from 1922 to 1941, over 50 species were described (in Diels's 1922 paper he almost doubled the number of species known from New Guinea by publishing 24 species that were new to science). In contrast, less than 10 New Guinea species have been published in the more than 60 years since. Very little mention is made regarding synonymy in any of the papers on New Guinea taxa and it is possible that some of the 100 taxon names will be sunk as future research finds them to be conspecific. Royen (1982), for example, estimates there to be c. 50 species in New Guinea. *Saurauia* appears to be

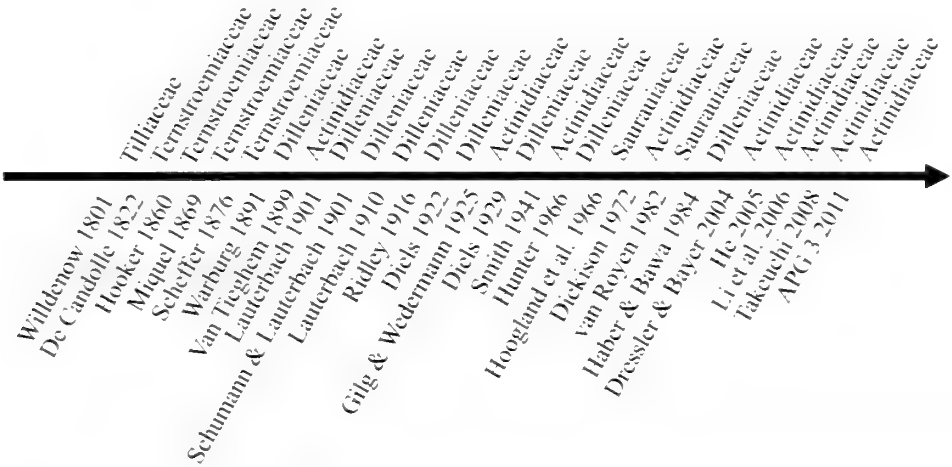

Fig. 1. A small selection of different family names under which *Saurauia* has been published.

particularly species-rich in New Guinea when compared with other areas: there are 6 species in Vietnam, 13 in China, 10 in Peninsular Malaysia (and the whole of the New World only has c. 60 species in total) (Cuong et al. 2007, Li et al. 2006, Rafidah Rahman, pers. comm. 2010, Hunter 1966 and Soejarto 1980, respectively). Many New Guinean *Saurauia* species appear to favour disturbed or partially disturbed habitats—the edges of clearings and trails for example. New Guinea is a very geologically active area, where frequent earthquake disturbances and landslips may provide a plethora of suitable habitats and may go some way to explaining the level of species diversity seen there.

Fig. 2 gives an overview of the number of taxon names published from New Guinea by year and, when considered alongside the fact that there is a substantial amount of indeterminate *Saurauia* material from New Guinea in herbaria around the world, suggests that the *Saurauia* of this region have been somewhat neglected in recent years. The reasons for this are perhaps manifold—the revisions are outdated—a significant number of species have been described since they were published and these new taxa are not included in the keys. There may also be a significant number of new species yet to be recognised as such. Smith (1941) noted that only a few *Saurauia* species (usually those occurring in lowland rain forest) were abundant, with most taxa from altitudes higher than 1200 m occurring in very narrow ranges. Many of the indeterminate specimens have been collected from high altitude areas previously not researched botanically.

Saurauia in New Guinea have long since been considered a 'difficult' group to work with due to the lack of a solid and taxonomically sound generic framework around which new taxa can be added. There is no definite understanding of which characters are taxonomically significant. Recent studies on New World taxa (by Soejarto in 1980), however, are promising and may hold the key to bringing a sense of order to the New Guinea taxa. The distribution of indumentum on sepals and also the type of indumentum on different plant parts has been found to be taxonomically significant. This may also be true of the New Guinea taxa where a wide variety of

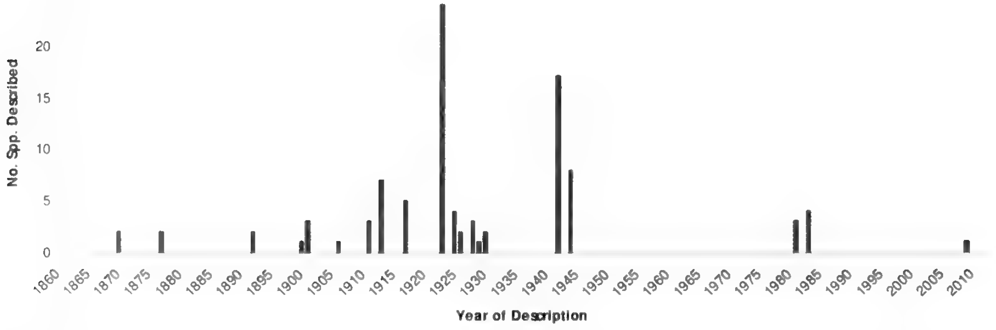

Fig. 2. The number of *Saurauia* species described for New Guinea each year, the first by Miquel in 1869, the last by Takeuchi in 2008.

indumentum is evident and should be a consideration of any future research on the group in New Guinea.

The long reaching aim of future work on *Saurauia* taxa from New Guinea will be to look for taxonomically significant characters that can be used to identify species, to write a comprehensive key to the species and to get an overview of how these species relate to others in the Flora Malesiana region. No molecular studies have been published to date and such work may yield useful information when looked at in parallel with morphological studies. There is evidently much to learn about the genus *Saurauia* in New Guinea and it is hoped that, with careful research and access to herbarium specimens, DNA samples, field notes and photographs, definite progress towards these aims can be made.

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Searching for Sumatran *Begonia* described by William Jack: following in the footsteps of a 19th century Scottish botanist

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ABSTRACT. Eight species of *Begonia* were described from Sumatra in 1822 by the Scottish botanist William Jack. All of the type material associated with these names was destroyed in a fire in 1824, and an expedition was mounted in August 2010 to re-visit Jack's collecting localities in an effort to find material suitable for neotypification. Of the eight species, two (*Begonia bracteata* Jack and *B. racemosa* Jack) could be neotypified with certainty, whilst others require further work. It is possible that some of the species described from Bengkulu province may have become extinct due to loss of forest habitat.

Keywords. *Begonia*, Sumatra, William Jack

Introduction

William Jack (1795–1822) was the son of the Principal of Aberdeen University. He is celebrated as "one of the most able botanists ever to become associated with the incredibly rich and the then very little known flora of the Malay Peninsula and Archipelago" (Merrill 1952). According to Don (1834), his "well known indefatigable labours in natural history have long ago entitled him to the highest respect" and tribute has been paid to "the astonishing accuracy of [his] work and his descriptive powers" (Noltie 2009). Two tragedies throw these accolades into relief; Jack's untimely death at the age of 27, and the destruction of the bulk of his biological collections by fire.

After finishing his medical training in London, Jack left England for India in 1813 to work for the British East India Company as a surgeon. Whilst in India he commenced correspondence with Nathanial Wallich in Calcutta, who recommended Jack to Sir Stamford Raffles as a suitable appointment to his staff as both a medical man and botanist. This appointment led Jack to Sumatra, where the British East India Company was hoping to strengthen its influence, and where Jack would be able to make his name as one of the most prolific and brilliant botanists of his time. He made collections from the island during 1819–1822, visiting North Sumatra (Tapanoeli), West Sumatra (Pulau Pegang and neighbours, and the Nias Islands) and Bengkulu (Gunung Bungkuk and the interior of the province). Jack published a fascinating account of his 1821 ascent of Gunung Bungkuk ("Gunong Benko" or "Sugar Loaf Mountain"; Jack 1822a), where locals pleaded with Jack and his party not to climb the mountain, as they feared the vengeance of evil spirits if they achieved the sacred summit. However, he was undaunted:

> "The next acclivity terminated at the head of another ravine, where their progress was again checked by a jutting rock rendered moist by the trickling of a small spring of water from among its crevices. Here the guides declared that further ascent was impracticable, and that from thence the party might return as soon as they pleased. The fact is, they were extremely averse to their proceeding, fearing the vengeance of the evil spirits if they conducted strangers to the summit; they were, therefore, advising to return at every difficulty, and the ascent was ultimately accomplished without their aid, or rather in spite of them."

And reached the summit in spite of the very difficult terrain:

> "The last of these precipices was perhaps the most dizzy and dangerous, as it was necessary to make a step or two on a narrow ledge on the face of a cliff of such height that the eye could not discern the bottom, and thence catch at a dry stump barely within reach, by swinging from which it was possible with a considerable effort to clear the rock. The denseness of the moss and the stunted appearance of the trees now indicated their approach towards the top, and at length about two o'clock they found themselves on the summit. This was a bare spot of not more than four or five yards in breadth with a precipice on each side partly concealed by brushwood. Of those who set out together from the foot of the hill a few only reached this point, by far the majority giving up in despair at different parts of the ascent, but the labour of those who persevered was amply recompensed by the view which opened from the summit."

Within a year, two of the three "mountain defilers" (Noltie 2009), Captain Harry Auber and Jack himself, were dead. Jack contracted malaria during an excursion to Moco-Moco in March 1822, which in combination with the consumption caught during his time in Nepal proved more than his health could bear. His condition became so grave that he was placed on a passage to England aboard the *Layton*; however the departure was delayed to bad weather and due his rapidly deteriorating condition, Jack was moved to Government House in Bengkulu, where he died shortly after. As if to further avenge the trespass, in 1824 all of Jack's wonderful collections were lost. Raffles had them loaded on the *Fame* along with other irreplaceable manuscripts and drawings and set sail from Bengkulu on the 2nd of February 1824. Allegedly the ship caught fire after a sailor tried to illicitly tap a brandy cask by candle light; all onboard were saved but the entirety of the collections were lost, an enormous tragedy for Malesian botany second only to the death of Jack himself.

In his short career, Jack managed to describe about 200 species and 31 genera of plants. His account of the *Begonia* he collected on Sumatra was published in 1822 in *Malayan Miscellanies* (Jack 1822b):

> "The island of Sumatra abounds with *Begoniae*, a tribe of plants which are chiefly found in moist shady situations at the foot of hills and in the recesses of forests. Being succulent herbs they are with difficulty preserved in herbaria, and the specimens are frequently deficient in one or other of the parts of fructification. Descriptions from the living plants in their native soil are therefore particularly desirable, and in this view the following account

of the species which have fallen under my observation will not be uninteresting."

The loss of Jack's collections, of which only a few scraps reached Europe prior to the *Fame* disaster, means that vast majority of his plant names have no type material, and this is certainly true for his *Begonia* names. Although Jack had a deserved reputation for writing excellent descriptions, the variation between *Begonia* species on Sumatra can be subtle, and the absence of any comparative diagnoses in Jack's account means neotypes are a necessity to fully understand the application of his names. To this end, the authors undertook an expedition during August 2010 to re-visit the localities where Jack collected *Begonia* specimens, in an attempt to find material suitable for neotypification. The expedition was based, firstly, in Padang, then Bengkulu (Fig. 1). This permitted collecting on Pulau Pasumpahan and Gunung Bungkuk, and in the rapidly diminishing remaining forest scattered throughout Bengkulu province. The trip to Gunung Bungkuk was navigated using Jack's 1822 manuscript and we used the same village as a base, Rejak Bessi. The dense forests which obscured Jack's view of the mountain have now been cleared (Fig. 2), allowing us to reach the base of the mountain in less than one hour with the aid of motorcycles with tyre chains. It was possible to reach the mountain and return to Bengkulu in the same day, in contrast to Jack's expedition which lasted eight days in all. Another contrast to Jack's expedition is that a full ascent was not attempted, due to failing light and a desire by the participants not to suffer the same fate as their 19th century predecessors. The fact that the expedition took place during the Muslim fasting month was another, minor, consideration, although by the time of the descent the elusive *Begonia bracteata* plus another new species had been found.

Taxonomic treatment

Sectional placement

Following examination of descriptions, herbarium specimens and living plants, insights have been gained to allow a more informed sectional classification of Sumatran *Begonia*, leading on from the excellent groundwork laid down by Doorenbos et al. (1998). *Begonia caespitosa*, *B. orbiculata* and *B. sublobata* are transferred from *Begonia* sect. *Diploclinium* to *Begonia* sect. *Reichenheimea*; the former section is no longer represented on the island and the latter probably represents a local radiation, possibly including some species from Peninsular Malaysia such as *B. forbesii* and allies. *Begonia* sect. *Reichenheimea* is currently united by the presence of entire placentae and, on Sumatra at least, a functionally scapigerous habit. The Sumatran species and their allies may eventually require a section of their own to accommodate them, depending on further study of the type of the section, *B. tenera* Dryand. from Sri Lanka. Jack's suggestion of a resemblance of *Begonia sublobata* to *B. grandis* is most definitely not supported. *Begonia fasciculata* and *B. pilosa* are transferred from *Begonia* sect. *Petermannia* to *Begonia* sect. *Bracteibegonia*, due to the presence of red hairs on the leaves which is so characteristic of the section on Sumatra. *Begonia* sect. *Bracteibegonia* seems to be much more species rich on Sumatra than *Begonia* sect.

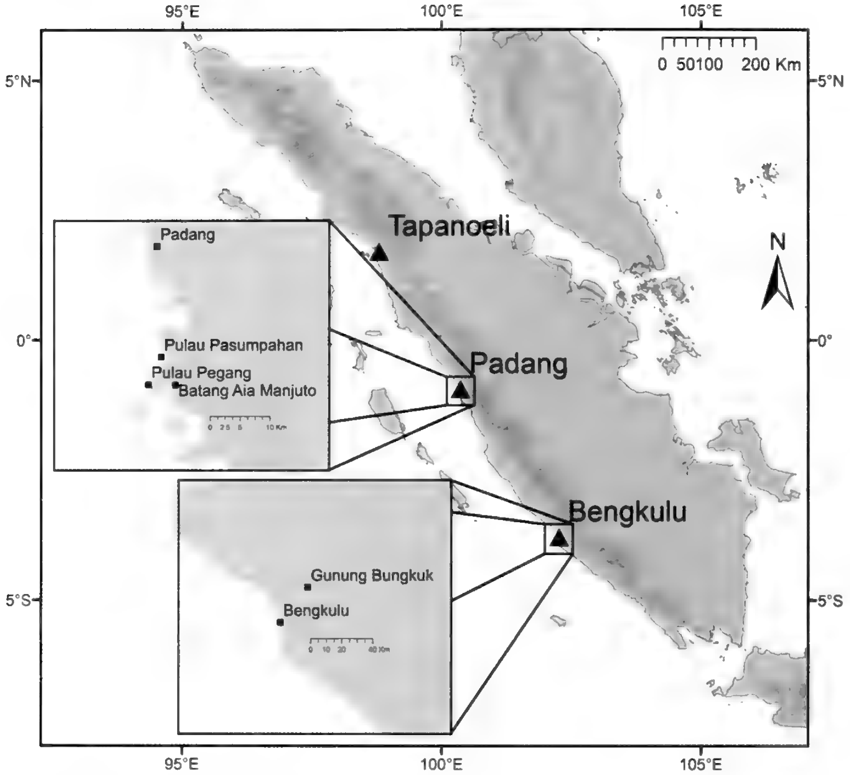

Fig. 1. Map of Sumatra showing localities mentioned in the text.

Fig. 2. The isolated peak of Gunung Bungkuk, approximately 30 km northeast of Bengkulu town.

Petermannia, which is characterised by being glabrous and having larger inflorescences. *Begonia racemosa* and a *B. geniculata* remain in *Begonia* sect. *Petermannia*.

Species descriptions

Jack's original descriptions and diagnoses (Jack 1822b) are reproduced here, arranged first by current sectional placement and then alphabetically. Following each is a discussion of the success or failure to find a neotype, and where possible, an account of comparative diagnostic characters to related taxa.

Begonia bracteata Jack [§ *Bracteibegonia*], Malayan Misc. 2(7): 13 (1822); Miquel, Pl. Jungh. 417 ('1855', 1857); Candolle, Prodr. 15(1): 316 (1864); Golding, Phytologia 54(7): 494 (1984). *Diploclinium bracteatum* (Jack) Miq., Fl. Ned. Ind. 1(1): 688 (1856). TYPE: Sumatra, Bengkulu Province, Gunung Bungkuk, 3°35'3"S 102°25'24"E, 610 m, 15 Aug 2010, *D. Girmansyah & M. Hughes DEDEN1495* (neotype here designated BO; isoneotypes ANDA, E, K, SING). (Fig. 3)

Foliis duplicato-serratis acuminatis pilosis, pedunculo 1–3 floro bracteis numerosis appressis vestito, capsulis basi bibracteatis; alis equalibus rotundatis.

Near the foot of Gunong Bunko in the interior of Bencoolen.

Suberect, strong and branching, very villous, shaggy. Leaves alternate, short petioled, ovate, semicordate at the base, acuminate, duplicato-serrate, pilose, 3–4 inches long. Stipules large, pilose. Peduncles oppositifolious, generally supported by a smaller leaf, invested particularly towards the base with many pair of opposite ovate acute pilose ciliate bracts, which are pressed flat against each other; the uppermost pair is distant from the rest and supports from one to three pedicels. Flowers white. Male. Corolla four petalled; the outer two large subrotund. Stamina numerous. Female. Corolla five petalled; petals nearly equal. Styles three. Stigmata lunate, villous with yellow short glandular hairs. Capsule embraced by two bracts at the base, three celled, three winged; wings equal, rounded.

Notes. Neotypification was very straightforward for this species, due to the precise locality and this being the only *Begonia* sect. *Bracteibegonia* in the vicinity, in addition of course to matching the clear description perfectly. This species has been considered a synonym of *Begonia lepida* Blume from Java (Koorders 1912), but is a much hairier plant; Jack's description as 'shaggy' is very apt; it differs in having much longer, erect, translucent hairs on the stem (not reddish appressed hairs), hairier stipules, noticeably bullate leaves and also lacks any red colouration on the stems, leaves and young tepals. It is similar in habit and leaf shape to an undescribed species from Aceh (*Wilkie et al. PW621a*, Gunung Leuser National Park, Ketambe Research Station, BO, E, SING), which differs in having appressed, matted, red hairs rather than erect, translucent hairs on the stem; differences between this taxon and *Begonia lepida* (considered endemic to Java) need to be clarified.

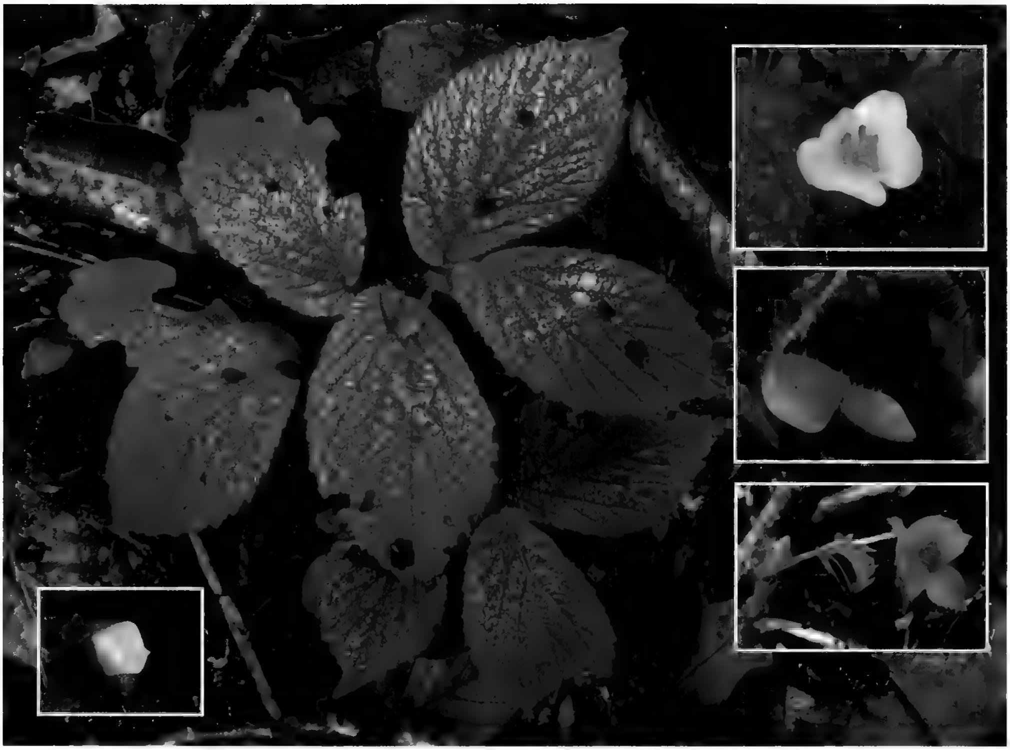

Fig. 3. *Begonia bracteata* Jack. Main image, habit; top right, female flower; middle right, female flower after pollination; bottom right, female flower with developing fruit; bottom left, opening male flower. All from *DEDEN1495*, Gunung Bungkuk, Bengkulu.

IUCN category: In the absence of collections from elsewhere, it is assumed that this species is endemic to Gunung Bungkuk and nearby forests. As the foothills have been cleared of forest for coffee plantations up to the base of the mountain, *Begonia bracteata* will have undergone a significant contraction in range since Jack's expedition, and is now effectively endemic to the slopes of the mountain itself. The steepness of the terrain will afford some protection, but as the forests on Gunung Bungkuk do not belong to a formally designated protected area, *B. bracteata* should be considered as Vulnerable (VUD2).

Begonia fasciculata Jack § [*Bracteibegonia*], Malayan Misc. 2(7): 12 (1822); Candolle, Prodr. 15(1): 322 (1864). *Petermannia fasciculata* (Jack) Klotzsch, Monatsber. Kon. Preuss. Akad. Wiss. Berlin 1854: 124 (1854); Klotzsch, Abh. Kon. Akad. Wiss. Berlin 1854: 195 (1855); Klotzsch, Begoniac. 75 (1855). *Diploclinium fasciculatum* (Jack) Miq., Fl. Ned. Ind. 1(1): 690 (1856). TYPE: Sumatra, Tappanuly, *Jack* (destroyed).

Foliis inferioribus alternis, stiperioribus oppositis, oblongo-ovatis basi semicordatis duplicato-serratis pilosis, perianthiis masculis diphyllis, capsulae alis equalibus obtusangulis.

Found at Tappanuly on the west coast of Sumatra.

Caulescent. Stem weak, jointed, thickened at the joints, round, covered with red hairs. Leaves petiolate, the lower ones alternate, the upper ones opposite, oblong-ovate, inequilateral, semicordate at the base, acuminate, irregularly serrate, covered above with red erect subspinescent hairs, beneath with softer and weaker hairs. Petioles densely pilose. Stipules linear, acuminate, pilose. The flowers come in fascicles from the middle of the petioles, and these flower bearing leaves are always opposed to another without flowers; hence it is that the upper leaves are opposite while the lower are alternate. Fascicles composed of male and female flowers; pedicels slender, smooth, white. Bracts several at the base of the blades, acute, pilose, red. Male perianth diphyllous, white. Stamina numerous. Anthers yellow. Female perianth superior, white, cup-shaped five leaved; petals ovate, acute, with a few short red hairs on the outside. Style deeply trifid lobes convolute, infundibuliform. Capsule three-winged, three-celled, wings equal, obtuse-angled.

Notes. The specimen *Argent & Iqbar 9968* (E) from Tapak Tuan 250 km northwest of Tapanoeli is the closest match to this species, but does not have leaves "covered above with red erect subspinescent hairs". There are hardly any collections from the vicinity of Tapanoeli and the location was not on the itinerary for the 2010 expedition; the area needs to be further explored to search for suitable material.

IUCN category. Data Deficient.

Begonia pilosa Jack [§ *Bracteibegonia*] Malayan Misc. 2(7): 13 (1822). *Diploclinium pilosum* (Jack) Miq. Fl. Ned. Ind. 1(1): 688 (1856). TYPE: Sumatra, Bengkulu Province, *Jack* (destroyed).

Foliis subsessilibus irreguliter serratis acumiatis pilosis subtus rubris, bracteis ad basin pedicellorum subrotundis ciliatis, capsulae alis subaequalibus parallelo rotundatis.

Interior of Bencoolen.

Caulescent, pilose. Leaves alternate, scarcely petiolate, ovate, inequilateral, acuminate, slightly and irregularly serrate, pilose with long red hairs, under surface of a bright red colour; about three inches long. Stipules large, lanceolate, pilose externally. Peduncles oppositifolious, subidichotomous. Bracts at the base of the pedicels, roundish, ciliate. Flowers white. Male: Corolla four petalled, the inner pair smaller. Stamina numerous. Female: Corolla five petalled; the two outer petals larger. Capsule three winged; wings nearly equal, parallel and rounded.

Notes. In addition to *Begonia bracteata*, two other members of *Begonia* sect. *Bracteibegonia* were encountered on the expedition, represented by *D. Girmansyah*

& M. Hughes DEDEN1493 & DEDEN1507, both collected in Bengkulu. Neither have large stipules, one has leaves which are glabrous above and the other has leaves which are pilose but considerable less than three inches long, and hence neither can be ascribed to *Begonia pilosa* Jack. Examination of other specimens of this section in ANDA and BO also fails to provide a convincing match.

IUCN category. Data Deficient.

Begonia geniculata Jack [§ *Petermannia*] Malayan Misc. 1(7): 15 (1822); Candolle, Prodr. 15(1): 321 (1864). *Petermannia geniculata* (Jack) Klotzsch, Monatsber. Kon. Preuss. Akad. Wiss. Berlin 1854: 124 (1854); Klotzsch, Abh. Kon. Akad. Wiss. Berlin 1854: 196 (1855); Klotzsch, Begoniac. 76 (1855). TYPE: Sumatra, *Jack* (destroyed).

Caule geniculato, foliis ovato-oblongis denticulatis acuminatis glabris, pedunculis divaricato dichotomis, floribus superioribus masculis dipetalis, inferioribus femineis, capsulae alis equalibus obtus angulis.

Sumatra.

Caulescent; stems smooth, compressed, channelled, jointed, thickened at the articulations. Leaves alternate, petiolate, semicordate at the base, ovate oblong, acuminate, denticulate smooth. Peduncles oppositifolious, dichotomous, divaricate, many flowered, lower flowers female, upper male. There is often a female flower from the axil. Male perianth two petalled, white. Stamina numerous; anthers oblong, broader above. Female. Capsules long, three winged, wings obtuse-angled, equal, smooth.

Observations by Jack. The leaves of this plant are used by the natives for cleaning and taking out rust from the blades of creeses. It has considerable resemblance to the preceding species [*Begonia racemosa*].

Notes. The description of *Begonia geniculata* is uncharacteristically short for Jack, and it reads like a brief description of *Begonia* sect. *Petermannia* generally. Combined with the lack of a specific locality, it means this species will be near impossible to neotypify. It is feasible that its resemblance to *Begonia racemosa*, typified below, may be of some use in sorting out its true identity once *Begonia* sect. *Petermannia* becomes better known on Sumatra.

IUCN category. Data Deficient.

Begonia racemosa Jack [§ *Petermannia*] Malayan Misc. 2(7): 14 (1822); Candolle, Prodr. 15(1): 322 (1864). *Petermannia racemosa* (Jack) Klotzsch, Monatsber. Kon. Preuss. Akad. Wiss. Berlin 1854: 124 (1854); Klotzsch, Abh. Kon. Akad. Wiss. Berlin 1854: 196 (1855); Klotzsch, Begoniac. 76 (1855). *Diploclinium racemosum* (Jack) Miq., Fl. Ned. Ind. 1(1): 691 (1856). TYPE: Sumatra, Bengkulu Province, Bukit Menyan, 3°36'26"S 102°39'39"E, 1110 m, 19 Aug 2010, *D. Girmansyah & M. Hughes*

DEDEN1509 (neotype here designated BO; isoneotypes ANDA, E, K, SING). (Fig. 4)

Foliis obovato oblongis irregulariter dentatis acuminatis glabris, racemis erectis masculis, flore femineo axillari, perianthiis masculis diphyllis, capsulae alis equalibus parallelo-rotundatis.

Interior of Bencoolen.

Suberect; stem smooth, jointed. Leaves alternate, short petioled, obovate oblong, attenuated towards the base which is unequally cordate, acuminate, irregularly and unequally dentate, smooth; 6–7 inches long. Stipules large, oblong. Racemes oppositifolious, long, erect, bearing numerous fasciculate male flowers, and having a single female one in the axil. Male. Corolla two petalled, petals very thick. Stamina numerous. Female. Capsule with three equal parallel rounded wings, three celled.

Specimens: **Sumatra**. Bengkulu, Kaba, 1 Mar 1931, *C.N.A. de Voogd 1053* (BO, L); Bengkulu, Kaba, 10 Mar 1932, *C.N.A. de Voogd 1325* (BO, L); Bengkulu, Sungei Gembung, 100 m, 12 Oct 1993, *J.J. Afriastini 2620* (BO); Bengkulu, Sungei Gembung, 100 m, 12 Oct 1993, *J.J. Afriastini 2625* (BO); Bengkulu, Road from Kapahiang, 3°39'47"S 102°33'46"E, 660 m, 17 Aug 2010, *D. Girmansyah & M. Hughes DEDEN1498* (ANDA, BO, E).

Notes. Matching this name to collections was initially confounded by Jack's description of the inflorescences as *oppositifolius*, as in *Begonia* sect. *Petermannia* they are usually terminal, as was the case in all the specimens of this section collected during the expedition. However, one can easily interpret this terminal inflorescence syndrome as *oppositifolius* when considering a highly branched specimen (e.g., Fig. 4). This species was observed at three localities during the 2010 expedition (Bukit Menyan, Kapahiang and Bukit Kaba), and it seems likely therefore that Jack would also have happened upon it. They key characters are the leaf shape, the long inflorescences, the thick tepals of the male flower and the capsule with rounded wings, all of which match between the description and specimens *D. Girmansyah & M. Hughes DEDEN1498* & *DEDEN1509*. Strictly speaking the inflorescence is not racemose, but an elongated cyme. A further distinctive but previously unknown feature of *B. racemosa* is that the female flowers have three tepals, an unusual feature in *Begonia* generally.

IUCN category. Of the known populations of this species, only one is confirmed as being in a protected area (Bukit Kaba). One of the localities, Bukit Menyan, is not under protection and the already small forest fragment is under active encroachment from coffee plantations. However, it is extremely likely that *Begonia racemosa* is present in the extensive nearby Bukit Hitam protection forest, and as long as Bukit Kaba and Bukit Hitam remain in good condition the IUCN category Least Concern is considered appropriate.

Fig. 4. *Begonia racemosa* Jack. Main image, habit; top left, male flower; middle left, female flower, all from *DEDEN1509*, Bukit Menyan, Bengkulu. Bottom left, male portion of inflorescence, Gunung Kaba, Bengkulu.

Begonia caespitosa Jack [§ *Reichenheimea*] Malayan Misc. 2(7): 8 (1822); Candolle, Prodr. 15(1): 397 (1864). *Diploclinium caespitosa* Miq., Fl. Ned. Ind. 1(1): 685 (1856). TYPE: Sumatra, Bengkulu, *Jack* (destroyed).

Subacaulis, foliis inequaliter cordatis angulatis acuininatis glabris, pedunculis dichotome cymosis, capsulae alis equalibus obtusangulis v. rotundatis.

At Bencoolen.

Nearly stemless. Leaves petiolate, oblique, cordate at the base with rounded slightly unequal lobes overlapping each other a little, somewhat falcate, rounded and sublobate on one side, straighter on the other, attenuated into a long acumen or point, spinulose but scarcely serrated on the magin, smooth, shining above, pale and punctato papillose beneath; nerves 5–9, branched towards the margin. The leaves are of unequal size and vary somewhat in shape, the old ones being much rounder and more decidedly lobed than the younger ones, which have the point so much incurved as to be nearly falcate on one side. Petioles red, pilose. Peduncles often as long as the leaves, smooth, bearing a dichotomous cyme of white flowers. Bracts ovate, concave. Male perianth four leaved, the inner pair smaller. Stamina numerous, collected into a head. Female perianth superior, three leaved, two exterior large, subrotund, applied to each other as in the male flowers, and enclosing the third which is much smaller and oblong. Style trifid. Stimata lunato bifid, yellow and glanduloso-pilose. Capsule three winged, wings nearly equal, obtuse angled or rounded.

Notes. Four species in *Begonia* sect. *Reichenheimea* are represented by specimens from Bengkulu. Species A, with long petioles and large flowers (e.g., *D. Girmansyah & M. Hughes DEDEN1508*); species B, smaller with slightly lobed leaves (e.g., *D. Girmansyah & M. Hughes DEDEN1506*); species C, with peltate leaves (e.g., *de Voogd 1055*); and species D, with leaves mottled green and brown (e.g., *D. Girmansyah & M. Hughes DEDEN1496*). None of these match *Begonia caespitosa* perfectly; species B does have leaves which vary in the degree of lobing according to their age, but no evidence of falcate leaves was observed. The lack of size measurements in Jack's descriptions means none of the species can ruled out on what would otherwise have been a very simple character. It is possible, given its location ("*at* Bencoolen") that this is a lowland species which is no longer extant given the almost complete lack of indigenous forest cover on the vicinity of the coastal lowlands.

IUCN category. Data Deficient.

Begonia orbiculata Jack [§ *Reichenheimea*] Malayan Misc. 2(7): 9 (1822); Candolle, Prodr. 15(1): 398 (1864). *Diploclinium orbiculatum* (Jack) Miq., Fl. Ned. Ind. 1(1): 688 (1856). TYPE: Sumatra, Bengkulu, *Jack* (destroyed).

Subacaulis, foliis orbiculatis cordatis crenatis glabris, pedunculis subdichotomis, capsulae alis subequalibus obtusangulis.

Interior of Bencoolen.

Nearly stemless. Leaves petiolate, subrotund, from three to four inches in diameter, slightly oblique, cordate at the base where the lobes overlap each other, remotely crenate, rounded at the point, smooth except for the nerves of the under surface, beautifully and finely punctate above. Stipules scariose, acute. Peduncles erect, subdichotomous, nearly as long as the leaves, i.e. about six or eight inches in height. Flowers white. Male. Corolla four petalled, the outer pair large, oblong; the inner small. Stamina numerous. Female. Capsule three celled, many seeded, three winged; wings obtuse-angled, nearly equal.

Notes. As the inflorescences and flowers of many species of *Begonia* sect. *Reichenheimea* on Sumatra are extremely similar, we are left with only Jack's description of the leaf as diagnostic. Species D, collected from the base of Gunung Bunkuk, matches in having orbiculate crenate leaves, but differs in being distinctly bullate between the veins and being variegated green and purplish brown, rather than "beautifully and finely punctate". The bullate leaves on species D are very obvious, and it seems likely that

Jack would have noticed this; hence we assume there is no material available for the typification of *Begonia orbiculata*.

IUCN category. Data Deficient.

Begonia sublobata Jack [§ *Reichenheimea*] Malayan Misc. 2(7): 10 (1822); Candolle, Prodr. 15(1): 355 (1864). *Diploclinium sublobatum* (Jack) Miq., Fl. Ned. Ind. 1(1): 690 (1856). TYPE: Sumatra, West Sumatra, Pulau Pegang, *Jack* (destroyed).

Repens, foliis cordatis subquinquelobis vel angulatis dentato serratis margine reflexis glabris, capsulae alis equalibus obtusangulis.

Found under moist rocks on Pulo Pegang, West coast of Sumatra.

Repent with a thick knotty root. Leaves alternate, petiolate, cordate, sometimes unequally, large and broad, often six or seven inches long, angulate, sometimes with five acute lobes, sometimes nearly ovate, acuminate, dentato-serrate, edges recurved, very smooth, 5–7 nerved, finely punctate, the dots appearing elevated on the upper surface and depressed on the lower. Petioles 4–6 inches long, nearly smooth, furnished immediately below their junction with the leaf with a semiverticil of linear acute appendices or scales. Stipules large, ovate, rather laciniate towards the apex, one on each side the petiole. Peduncles axillary, erect, 6–8 inches long, red, very smooth, terminated by a dichotomous divaricate panicle of white flowers tinged with red. Bracts roundish. Male. Perianth four leaved, leaflets rather thick and fleshy, the two outer ones much larger and subrotund, before expansion completely enclosing the inner two, and having their edges mutually applied to each other in such a manner that they form an acute carina round the unexpanded flower. Stamina, numerous in a roundish head; filaments short, inserted on a central column which rises from the base of the flower. Anthers oblong, cells adnate to the sides of the filaments, bursting longitudinally. Female. Capsules with three equal obtusely angled wings, three celled, three valved, valves septiferous in the middle, sutures corresponding to the wings. Seeds numerous, attached to placentae which project from the inner angle of the cells.

Observations by Jack. The serratures are hard and cartilaginous and recurved in such a manner along with the margin of the leaf, that when only observed on the upper surface their place is perceived by an indentation. It seems to resemble the *B. grandis* Dryand which differs however in having oblique, doubly serrated leaves, and purple flowers.

Notes. A photograph of a plant with red scales at the petiole apex, a unique character in Sumatran *Begonia* and diagnostic for *Begonia sublobata*, led us to Pulau Pasumpahan (Nurainas, pers. comm.), 5 km from the type locality of Pulau Pegang (Fig. 1). About 20 m back from the beach the (limestone?) rocky core of the island proved to be covered on one side with a *Begonia* species which appeared to match *Begonia sublobata* Jack

Fig. 5. *Begonia* sp. aff. *sublobata* Jack. Main image, habit; inset, top left, apex of petiole and leaf underside; top right, male flower; bottom right, female flowers and ovaries; bottom left, juvenile plant showing leaves with reduced lobing. All from *DEDEN1486*, Pulau Pasumpahan, West Sumatra.

in every detail (Fig. 5). This is one of Jack's more lengthy and detailed descriptions, and every character seemed to tally perfectly: the lobed leaf shape, the cartilaginous serratures on the leaf margin, the semiverticil of scales at the petiole apex, the fleshy outer tepals on the male flower, each of which is diagnostic enough when considered singly. However, in the excitement of the moment of discovery, the authors failed to notice that the collection from Pulau Pasumphan did not have leaves which were "finely punctate, the dots appearing elevated on the upper surface and depressed on the lower": they were completely smooth. However by the time this was noted several days had passed and there was no time to visit Pulau Pegang to investigate further. Another species, as yet unnamed and manifestly allied to *Begonia sublobata* given the red scales at the petiole apex, was discovered nearby on the mainland at Batang Aia Manjuto. Hence it seems possible that the ancestor of *Begonia sublobata* has fragmented locally into a number of taxa, and that the islands in the bays south of Padang may harbour a number of endemic species. Consequently further work is required to resolve the true identity of *Begonia sublobata*.

IUCN category. Data Deficient.

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Materials for a revision of *Erycibe* (Convolvulaceae) in Peninsular Malaysia

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ABSTRACT. Information from the literature, new observations based on field study, and new distribution data gathered from herbarium specimens and new collections are assembled in preparation for a revision of the genus *Erycibe* in Peninsular Malaysia. Significant new data are discussed and a conservation status is assigned to each of the 19 taxa recognised in Peninsular Malaysia. Problems still to be resolved are highlighted.

Keywords. Convolvulaceae, *Erycibe*, Peninsular Malaysia

Introduction

Erycibe includes about 75 species distributed mainly in tropical Asia and Malesia with outlying species in Australia, Japan and Taiwan (Staples 2010). The genus *Erycibe* was first described by Roxburgh (1798), based on *E. paniculata* Roxb. from India. The taxonomic framework for understanding the genus was established by Hoogland (1953a) who provided a nomenclatural review of all taxa described at that time (70 accepted species). Detailed descriptions, keys for identification, selected illustrations, ecological information and biogeographical distribution summaries were provided for the 53 Malesian species (Hoogland 1953b). Later, an index of all *Erycibe* specimens examined was prepared (Hoogland 1961) that remains useful for naming older herbarium specimens and is invaluable for understanding the taxonomic concepts Hoogland employed. Subsequent to Hoogland's work another five Asian species have been described although not all are accepted.

Hoogland made a thorough revision based solely on herbarium material and his keys and descriptions rely heavily on reproductive (floral) characters. He was the first to use trichome characters, particularly the hairs from the calyx and the midpetaline bands, to distinguish the species in certain groups. Yet, while the keys and descriptions work well enough in the herbarium, they are not practical for field identification. Using the hair characters requires a compound microscope with an optical micrometer for measuring accurately; many botanists and collectors have lamented the lack of good field characters for recognising *Erycibe*. This is problematic especially when trying to key out sterile or fruiting materials.

In the account of *Erycibe* in Peninsular Malaysia, Ridley (1923) recognised 15 species, documented in the *Flora of the Malay Peninsula*; some of these were later reduced to synonymy by Hoogland (1953a, 1953b). Hoogland accepted 16 species and 2 varieties in Peninsular Malaysia. Of these, four taxa were considered endemic (*E. magnifica, E. praecipua* ssp. *praecipua, E. sapotacea* and *E. strigosa*). Later, Ng (1989) recognised two more species that he named 'species A' and 'species B' based on leaf characters. Until now, the two latter species have not been described due to incomplete material. In total, Peninsular Malaysia has 19 recognised taxa.

Almost six decades after Hoogland's revision for *Flora Malesiana,* there is no updated taxonomic revision for the genus *Erycibe* in Peninsular Malaysia. The Flora of Peninsular Malaysia Project now provides an impetus to re-examine the genus and synthesise new information. Today, there are more collections of *Erycibe* available, which makes it possible to review taxonomic concepts for the recognised species and the two new taxa recognised by Ng. The full revision of the genus in Peninsular Malaysia, with a new key, detailed descriptions, distribution maps for each species and colour photographs will be published in the Flora of Peninsular Malaysia account. The purpose of the present paper is to bring together new information gathered from the literature, from field observations of living plants, and from study of the herbarium specimens that have accumulated since the 1950s. Furthermore, the conservation status for each species has been assessed based on the Malaysia Plant Red List Guideline (Chua & Saw 2006).

Materials and methods

Field study and specimen collection

Nine field trips were carried out from January 2009 till April 2010 at known localities as well as in new collection areas, while specialised trips were carried out to relocate rare species to obtain fresh materials. Materials for flowers and fruits were preserved in the spirit collection in addition to voucher specimens. Further information of the habitat and habit characters based on personal observations made in the field was added. In addition, close-up colour photographs were taken, especially of flower and fruit parts, as an aid in distinguishing the species.

Comparative morphology based on herbarium specimens

This study was conducted on herbarium specimens from the following herbaria: BKF, K, KEP, KLU, L, SING and UKMB. A total of 586 specimens of *Erycibe* collected from Borneo, Singapore, Sumatra and Thailand were borrowed and compared with specimens collected from Peninsular Malaysia. Of these, 241 collections of *Erycibe* collected from Peninsular Malaysia were examined.

Scanning Electron Microscope (SEM) studies

The structures of the floral parts, especially trichomes on the mid-petaline bands and calyx, have been observed by Hoogland (1953b) to be of taxonomic value for distinguishing the species. However, during that time, Hoogland observed this character through light microscopy and no figures or plates were provided in his account to illustrate this character. Today, Scanning Electron Microscope (SEM) offers a powerful technique for observation of trichome characters and making precise measurements. In this study, 15 species were studied using Scanning Electron Microscope (FEI Quantum 200) using herbarium specimens or fresh materials.

Conservation status of Erycibe

The distribution of the Peninsular Malaysian *Erycibe* species has not been mapped, so their conservation status is unknown, particularly for the endemic species. The conservation status assessment of each taxon is being carried out based on the guidelines and criteria of the Malaysia Plant Red List (Chua & Saw 2006). The final result for all 19 taxa is currently in preparation.

Results and discussion

Distribution of Erycibe

Based on the data from recently collected material together with that on herbarium specimen labels, all *Erycibe* species are found and distributed in lowland to hill forest, ranging from 20 m to 1200 m a.s.l. From the field work conducted, only four of the 19 taxa, namely, *E. albida*, *E. sapotacea*, *E. stapfiana* and *E. rheedii* were found and studied in the forest at the base of Gua Wang Buluh and Temurun Waterfall (Kedah state), Penang Hill (Penang), base of Gunung Korbu and Bubu Forest Reserve (Perak), Forest Research Institute Malaysia (Selangor), Pasoh Forest Reserve (Negeri Sembilan), Gunung Belumut (Johor) and Tembat Forest Reserve (Terengganu) (Fig. 1).

Erycibe albida was found flowering at Temurun Waterfall (Kedah), Pasoh Forest Reserve (Negeri Sembilan) and Tembat Forest Reserve (Terengganu). All collections were made in lowland areas. However, no fruits were obtained.

Erycibe sapotacea was again found on Penang Hill (type locality). It has been recorded as endemic to Peninsular Malaysia in the past. Unfortunately, no flowers were obtained (December 2009). However, specimen *W.J.J.O. de Wilde & B.E.E. de Wilde-Duyfjes 21199*, 29 July 1981, from Sumatra (deposited in the Leiden herbarium) looks similar to *E. sapotacea* in fruit and leaf characters. For the time being, *E. sapotacea* is considered as an endemic to Peninsular Malaysia. However, further study is needed and perhaps this species has a wider distribution extending to Sumatra.

Erycibe stapfiana was observed flowering in April at the lower trail to Gunung Korbu (Perak). The flowering season is about 2–3 weeks only. It is a climber, reaching 30–35 m tall in the forest canopy. We found this climber on a hillside near a Saraca stream, which is relatively undisturbed with quite an open forest canopy.

Erycibe rheedii was found to be quite common in Pulau Tuba (Kedah) near Gua Wang Buluh (a limestone cave). It occurs along the trail to the cave's base. Similar to other species, *E. rheedii* also favours gaps where sunlight is available. From

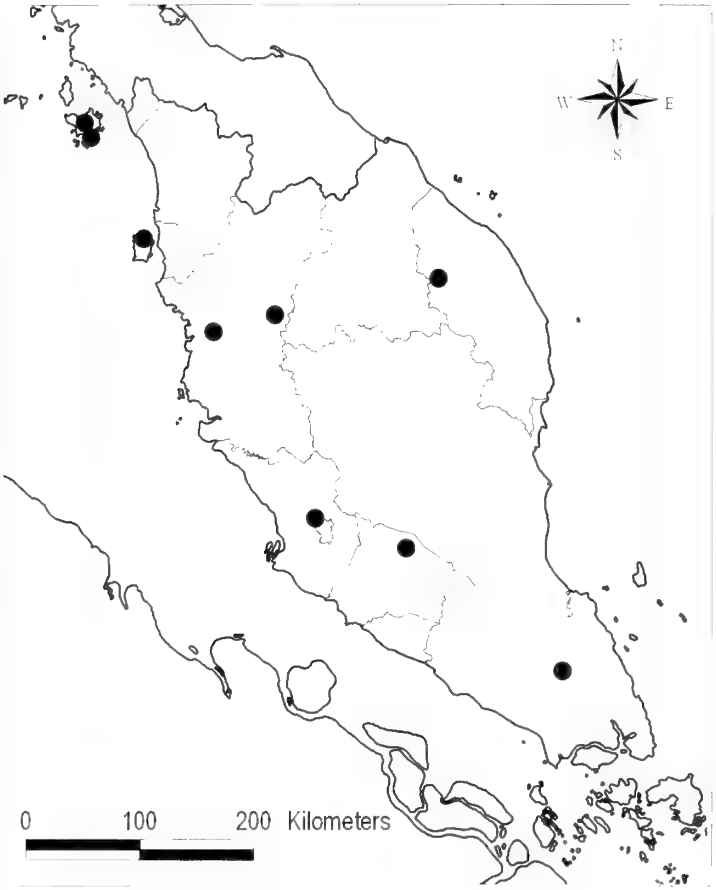

Fig. 1. Location of field collecting trips for *Erycibe* spp.

our observations, it only flowers once a year (early March) and the fruiting season is towards the end of the month.

Based on the data gathered, the distribution of the two undescribed species is now known. *Erycibe* sp. A is believed to be endemic to Gunung Belumut, Johor, and *Erycibe* sp. B is endemic to lowland forest of Pahang, Selangor and Negeri Sembilan.

Morphological observations

Generally, *Erycibe* species are small shrubs, woody climbers or lianas, climbing by twining high in the forest canopy. Plants are always found on forest margins, in forest gaps and sometimes near roadsides. In Peninsular Malaysia, only *E. albida* has been recorded consistently as a shrub. From the observations made in the field, the outer bark is normally light or pale grey, sometimes with lenticels or low longitudinal ridges and sometimes very smooth when the climbers become huge. However, characters such as plant height, bark texture and bark colours are not good taxonomic characters for identification because they are related to age of the climbers. Nevertheless, these characters are able to provide supplementary evidence for field identification.

As for the leaves, there are a few characters that are quite useful for the identification of Peninsular Malaysia species. The size and shape of the lamina in *E. leucoxyloides* is very distinct, oval-elliptic to lanceolate, 1.1–3.9 cm long and 0.5–1.3 cm wide. In the examination of herbarium specimens, some of the species such as *E. magnifica* have very clear venation underneath with thick pubescence. These characters are very consistent and can be useful to distinguish the species.

Erycibe has two types of inflorescence: racemose paniculate or glomerulate at either a terminal or axillary position. Many *Erycibe* species have very light sweet-scented flowers like jasmine, although there is a species recorded with a strong odour: *E. rheedii*. The flower of *Erycibe* is either white or creamy in colour. *Erycibe* has a deeply 5-lobed corolla, with each lobe having a bilobed apex and very dense hairy outside on the mid-petaline bands. The filament is either triangular or laterally concave. A few species have truncate anther and many have acute anther apices.

The fruit is a berry, with a little flesh surrounding the single seed, seated on the persistent calyx. Generally, the shape of the fruits is ovoid or ellipsoid or sometimes obpyriform. In Hoogland's revision for *Flora Malesiana*, important characters such as colour of the fruits was unknown for some species. For example, a recent collection made from Penang Hill added another important character for *E. sapotacea*: this species has pale grey fruits, which was not mentioned in Hoogland's account.

Micromorphological observations

For first time SEM technique is used for the micromorphological study on trichome structure of the midpeline bands and calyx. In this study, two main hair types were found on the midpetaline bands: two-branched hairs and three- to many-branched hairs (stellate hairs). Two-branched hairs are found in *E. festiva* and *E. maingayi*. Three- to many-branched hairs are found in other species and also in *E. maingayi*. For the calyx, a glabrous calyx surface is found only in *E. albida*, while two-branched hairs are found in *E. festiva*, *E. griffithii* and *E. maingayi* and three- to many-branched hairs (stellate hairs) are found in other species. Thus, the results from the SEM images support Hoogland's findings in 1953.

An examination of the mid-petaline and calyx hairs of the specimen *Sidek bin Kiah SK513*, 19 February 1976, from Kuala Dipang Forest Reserve, Perak (with very typical *Erycibe* leaf shape) shows it belongs to *E. festiva*, which has two- branched hairs. Initially this specimen had been wrongly identified as *E. griffithii* by the collector and later identified by an unknown person (in 2008) as *E. maingayi*.

However, from the analysis made, not all species can be distinguished by the trichome type. Trichome type is an additional character useful to distinguish a few species only.

Ecology and life history

In the study of plant dispersal by Ridley (1930), birds are reported as seed dispersers of *Erycibe tomentosa* var. *tomentosa* (synonym *E. princei*) and *E. malaccensis*. *Erycibe tomentosa* var. *tomentosa* produces large panicles of drupes; the fruits do not all ripen at once. The contrast of bright-orange unripe fruits (very conspicuous) with dark red or almost black ripe fruits is attractive to frugivorous birds. Besides that, there are anecdotal records by some biologists observing hornbills eating *Erycibe* fruits. However, recent books on hornbill biology such as Kinnaird & O'Brien (2007) and Poonswad (1998) do not list *Erycibe* (or any Convolvulaceae) among the food plants eaten by hornbills. Besides birds, the fruits of *Erycibe* are also eaten by mammals and McConkey & Galetti (1999) reported the sun bear (*Helarctos malayanus*) eating *E. maingayi* fruits and dispersing the seeds in Central Kalimantan, Indonesia. . The bear's droppings contained establishing *E. maingayi* seedlings found around 150 m from the adult liana.

Presently unresolved problems

After almost 60 years, the number of new herbarium collections for *Erycibe* in Peninsular Malaysia has not greatly increased. There were less than 100 collections of *Erycibe* collected after Hoogland's time. Several species, for example *E. strigosa*, has very little information known; the only collection is still only the type specimen collected in 1886 from Taiping, Perak, with very limited locality information. Therefore, further collecting would be important. Until now, incomplete material in herbarium specimens (fruits and flowers) prevents the description and formal naming of the two taxa recognised by Ng (1989). Besides, the locality data as stated on the specimen label are insufficient, thus it is hard to relocate the plant.

Even with new collections available, there are still major gaps to be filled, especially in life history data. The study of ecology, phenology, pollination, seed predation, herbivory, or seedling establishment is still lacking. Pollen grains have also still to be studied.

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Updating Malesian Icacinaceae

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ABSTRACT. The Icacinaceae were traditionally considered difficult to recognise because of extremely diverse vegetative anatomy and an enormous range in structure. Using a traditional circumscription of the family, the Icacinaceae of Asia were revised by Sleumer in 1969 and published in the Flora Malesiana in 1971, and included 100 species in 21 genera. Since the publication of the FM account, a new understanding of relationships within the group, stimulated by molecular phylogenetic data, has resulted in these genera being assigned to several different, more morphologically homogeneous families. In addition, an increase in collections has allowed species-level taxonomy to be revised in several groups, resulting in new species from the region, as well as a new genus from Borneo. In this paper these changes are reviewed, with a discussion of useful characters for identification, and an updated list of families, genera and species presented.

Keywords. Cardiopteridaceae, checklist, classification, Icacinaceae, Malesia, Stemonuraceae

Introduction

The Icacinaceae as historically circumscribed are a pan-tropical family of trees, shrubs and lianas with c. 50–55 genera and 300–400 species worldwide (Mabberley 1997, Kårehed 2001). However, recent studies have shown that the family as traditionally circumscribed was polyphyletic (Savolainen et al. 2000, Soltis et al. 2000, Kårehed 2002); this had resulted in a morphologically heterogeneous group that was difficult to recognise in the field and herbarium (e.g., van Balgooy 1998). Genera were traditionally placed in the family if they possessed a superior, unilocular ovary with two pendulous ovules, of which only one matures. In addition simple, exstipulate, alternate leaves, free petals with valvate aestivation, free stamens, and drupes with a single seed were used to identify members of the Icacinaceae. The family has now been split into five families residing in three different orders (see Kårehed 2001 and Stevens 2001 for an updated family classification).

The family was revised for the Flora Malesiana by Hermann Otto Sleumer (1971a), and our knowledge of the group in Malesia is based on this solid foundation.

Sleumer was best known for his work on Ericaceae and Flacourtiaceae, especially the former which he revised for the Flora Malesiana (published in 1966). His work on the Icacinaceae was something that he commenced in 1942 but, when compared to his treatments of Ericaceae, was considered a sideline, e.g., it has been noted that Sleumer's "taxonomic studies have included Ericales, Proteaceae, Flacourtiaceae, and various minor groups" (Doleshy 1966).

In addition to the new family limits, several new taxa have been described recently, including a new genus and a complete revision of the taxonomically complex genus *Gomphandra*, and these changes are summarised here with an updated key and checklist to the families in the Malesian region. We have kept the key to genera in Sleumer's original format as we note that many herbaria have yet to re-arrange their collections to a new APG III system and the collections will still be kept together in the traditional Icacinaceous circumscription. (We also feel that some botanists may still have a mental concept of Icacinaceae being those plants that are neither Euphorbiaceae, Flacourtiaceae nor anything else!) Distributions are given for each species following the TDWG distribution scheme (Brummitt 2001).

Key to the genera of
Cardiopteridaceae, Icacinaceae s.str., and Stemonuraceae in Malesia

The following key is adapted from Sleumer (1971a) with the new families in brackets after each genus, and with the addition of *Sleumeria*, *Cardiopteris*, and a brief distribution statement for each genus (distribution statements are given for each species below).

1a. Trees or (not climbing) shrubs 2
1b. Climbing shrubs or lianas, sometimes with tendrils. Flowers unisexual or functionally so 16

2a. Sepals essentially free at least in their upper 3/4 and imbricate 3
2b. Sepals connate into a cup-like calyx, its upper free part (or lobes), if any, short and not imbricate 6

3a. Flowers bisexual 4
3b. Flowers unisexual 5

4a. Petals free, valvate, or subimbricate in their upper part. Malesia (except Peninsular Malaysia) .... 2. ***Citronella*** [Cardiopteridaceae]
4b. Petals connate below into a tube, their upper part free and valvate in bud. New Guinea .... 4. ***Pseudobotrys*** [Cardiopteridaceae]

5a. Filaments free, fixed to the very base of the petals. Leaves with a layer of rounded to star-shaped appressed scales underneath at least in the young state. Malesia .... 11. ***Platea*** [Icacinaceae s.str.]

5b. Filaments adnate for almost their entire length to the lower tubular part of the petals. Scales absent. Malesia .... 3. ***Gonocaryum*** [Cardiopteridaceae]

6a. Flowers unisexual (or functionally so) 7
6b. Flowers bisexual 11

7a. Drupe ovoid-ellipsoid or oblongoid, without a fleshy lateral appendage. Flowers in rather short cymes. Malesia .... 19. ***Gomphandra*** [Stemonuraceae]
7b. Drupe laterally compressed (almond-like) 8

8a. Drupe without a fleshy lateral appendage. Flowers in spikes (very rarely in panicles composed of spikes, or almost fascicled). New Guinea and the Moluccas .... 14. ***Rhyticaryum*** [Icacinaceae s.str.]
8b. Drupe with a thick fleshy, laterally borne, practically entirely adnate appendage. Flowers in cymes 9

9a. Disk unilateral, thick-squamular. New Guinea ..... 20. ***Hartleya*** [Stemonuraceae]
9b. Disk absent 10

10a. Filaments glabrous. Fleshy appendage of drupe covering two pronounced ribs of the mesocarp. Philippines .... 18. ***Codiocarpus*** [Stemonuraceae]
10b. Filaments with apical, longish, club-shaped hairs at least in the fertile stamens. Prominent ribs under the appendage of the drupe less pronounced or absent. Malesia (except Borneo) .... 21. ***Medusanthera*** [Stemonuraceae]

11a. Ovary with a lateral swelling which in the fruit develops into a thick succulent appendage, appearing perpendicular to the drupe. Disk absent. Peninsular Malaysia to Philippines .... 5. ***Apodytes*** [Icacinaceae s.str.]
11b. Ovary and fruit without such an adnate appendage. Disk present or not 12

12a. Connective surpassing the anther cells as a marked glabrous apiculus. Outer part of the stone finally spongious-corky and deeply irregularly lacunose. Disk absent. Philippines and New Guinea .... 7. ***Merrilliodendron*** [Icacinaceae s.str.]
12b. Connective, if any, hardly or not surpassing the anther cells. Outer part of the stone fibrous, slightly ribbed or grooved lengthwise, or smooth outside 13

13a. Peduncle of inflorescence with numerous knob-like bracts which form alveoles. Stigma peltate. Disk absent. Sumatra, Peninsular Malaysia and Borneo .... 17. ***Cantleya*** [Stemonuraceae]
13b. Peduncle quite smooth. Stigma small, subcapitate or point-like. Disk ± cup-shaped 14

14a. Inflorescence usually terminal. Anthers glabrous. Philippines, Sumatra and Lesser Sunda Islands .... 9. ***Nothapodytes*** [Icacinaceae s.str.]

14b. Inflorescence axillary. Anthers with an apical tuft of club-shaped hairs 15

15a. Flowers sessile. Petals up to 8 mm, free to almost the base. Stigma point-like at the top of the ± attenuate (sometimes shortly style-like) part of the ovary. Malesia .... 22. ***Stemonurus*** [Stemonuraceae]
15b. Flowers 1–2 mm pedicelled. Petals (12–)13–15 mm, free in the distal part only. Stigma small on one side of the inverted, i.e. cup-like distal part of the ovary. Solomons .... 23. ***Whitmorea*** [Stemonuraceae]

16. Leaves opposite 17
16. Leaves spirally arranged 18

17a. Anthers broadly club-shaped to subglobular, many-celled, with numerous pollen-bearing alveoles. Moluccas, New Guinea and the Solomons .... 12. ***Polyporandra*** [Icacinaceae s.str.]
17b. Anthers as usual, with 2 cells. Malesia except New Guinea .... 6. ***Iodes*** [Icacinaceae s.str.]

18a. Twining liana with white milky juice. Flower bisexual (or with plants andromonoecious). Malesia .... 1. ***Cardiopteris*** [Cardiopteridaceae]
18b. Scandent shrubs, lianas. Plants dioecious (except *Sleumeria*) 19

19a. Flowers in elongate spikes or spike-like racemes, these solitary or sometimes composed of panicles 20
19b. Flowers in peduncled heads or umbels, these solitary or composed of racemes or panicles 22

20a. Leaves with rather lax but slightly raised reticulation. Sepals absent. Philippines .... 13. ***Pyrenacantha*** [Icacinaceae s.str.]
20b. Leaves markedly prominently tessellate on both faces. Sepals persistent 21

21a. Leaves glabrous or very sparsely hairy. Flowers usually 5-merous. Anther connectives not auriculate. Peninsular Malaysia to Philippines (including Java) .. .. 15. ***Sarcostigma*** [Icacinaceae s.str.]
21b. All parts hairy with yellow hairs. Flowers usually 4-merous. Anther connectives auriculate. Borneo .... 16. ***Sleumeria*** [Icacinaceae s.str.]

22a. Style absent, i.e. stigma sessile, thick-peltate. Peninsular Malaysia to the Philippines .... 8. ***Miquelia*** [Icacinaceae s.str.]
22b. Style (very) shortly thick-columnar, with 2–4 stigmatic lobes. Malesia .... 10. ***Phytocrene*** [Icacinaceae s.str.]

Checklist of Cardiopteridaceae, Icacinaceae s.str., and Stemonuraceae in Malesia

CARDIOPTERIDACEAE

A family difficult to characterise, but Kårehed (2001) lists free, imbricate sepals, sympetalous corollas, and epipetalous stamens as possible synapomorphies, which, together with no stipules, entire leaf margins and one seeded drupes, provide a combination of characters to help identify the family. The following genera and species are found in the Flora Malesiana region with the species composition unchanged since Sleumer (1971a, b).

1. *Cardiopteris* Wall. ex Royle
1.1. *Cardiopteris moluccana* Blume.
42 MOL, PHI, SUL; 43 BIS, NWG-IJ, NWG-PN, SOL-NO.
1.2. *Cardiopteris quinqueloba* (Hassk.) Hassk.
Distribution: 41 THA; 42 BOR-KA, JAW, LSI-BA, LSI-ET, LSI-LS, MLY-PM, SUL, SUM.

2. *Citronella* D.Don
2.1. *Citronella latifolia* (Merr.) R.A.Howard
Distribution: 42 PHI.
2.2. *Citronella philippinensis* (Merr.) R.A.Howard
Distribution: 42 PHI.
2.3. *Citronella suaveolens* (Blume) R.A.Howard
Distribution: 42 BOR-SB, BOR-KA, SUL, SUM, MOL; 43 NWG-IJ, NWG-PN.

3. *Gonocaryum* Miq.
3.1. *Gonocaryum calleryanum* (Baill.) Becc.
Distribution: 42 BOR-KA, MOL, PHI, SUL.
3.2. *Gonocaryum cognatum* Elmer
Distribution: 42 BOR-SB, PHI.
3.3. *Gonocaryum crassifolium* Ridl.
Distribution: 42 MLY-PM.
3.4. *Gonocaryum gracile* Miq.
Distribution: 42 MLY-PM, SUM.
3.5. *Gonocaryum impressinervium* Sleumer
Distribution: 42 BOR-KA, BOR-SR.
3.6. *Gonocaryum litorale* (Blume) Sleumer
Distribution: 42 LSI-ET, LSI-LS, MOL, SUL; 43 BIS, NWG-IJ, NWG-PN.
3.7. *Gonocaryum lobbianum* Kurz
Distribution: 41 THA; 42 MLY-PM.
3.8. *Gonocaryum macrophyllum* (Blume) Sleumer
Distribution: 42 BOR-BR, BOR-KA, BOR-SB, BOR-SR, MLY-PM, SUM.
3.9. *Gonocaryum minus* Sleumer
Distribution: 42 BOR-BR, BOR-SB, BOR-SR.

4. *Pseudobotrys* Moeser

4.1. *Pseudobotrys cauliflora* (Pulle) Sleumer
Distribution: 43 NWG-IJ, NWG-PN.
4.2. *Pseudobotrys dorae* Moeser
Distribution: 43 NWG-PN.

ICACINACEAE s.str.

The revised concept of Icacinaceae s.str. may be recognised by its racemose inflorescence of small flowers that are usually pentamerous (although they can be 4–6-merous); glabrous, alternipetalous stamens; unilocular ovary with 2 pendent ovules, and drupaceous fruits. In addition, the family is always woody (climbers or trees), the leaf margins are entire (although they can be palmately lobed) and exstipulate, but the leaves can be opposite or alternate. Apart from the description of the new genus *Sleumeria* (Utteridge et al. 2005) and a new species of *Platea* (Utteridge 2010), the members of this family are unchanged since Sleumer's (1971a) Flora Malesiana treatment. The genera *Phytocrene* and *Rhyticaryum* are the most likely candidates to yield new taxa or to have taxonomic changes made, especially the latter genus which has several species known only from a few collections from New Guinea.

5. *Apodytes* E.Mey. ex Arn.

5.1. *Apodytes dimidiata* E.Mey. ex Arn.
Distribution: 42 BOR-SB, JAW, LSI-LS, MLY-PM, MOL, PHI, SUM.

6. *Iodes* Blume

6.1. *Iodes cirrhosa* Turcz.
Distribution: 42 BOR-BR, BOR-SB, BOR-SR, JAW, ?MOL, MLY-PM, MLY-SI, PHI, SUL, SUM.
6.2. *Iodes ovalis* Blume
Distribution: 42 JAW, MLY-PM, MLY-SI, SUM.
6.3. *Iodes philippinensis* Merr.
Distribution: 42 BOR-BR, BOR-SB, MOL, PHI, SUL.
6.4. *Iodes reticulata* King
Distribution: 42 MLY-PM.
6.5.1. *Iodes velutina* King var. *velutina*
Distribution: 42 MLY-PM, MLY-SI.
6.5.2. *Iodes velutina* King var. *subvillosa* Sleumer
Distribution: 42 BOR-SR, SUM.
6.6.1. *Iodes yatesii* Merr. var. *yatesii*
Distribution: 42 SUM.
6.6.2. *Iodes yatesii* Merr. var. *glabrescens* (Ridl.) Sleumer
Distribution: 42 BOR-SR.

7. *Merrilliodendron* Kaneh.

7.1. *Merrilliodendron megacarpum* (Hemsl.) Sleumer
Distribution: 42 PHI, SUL; 43 BIS, NWG-IJ, NWG-PN, SOL-NO, SOL-SO.

8. *Miquelia* Meisn.
8.1. *Miquelia caudata* King
Distribution: 42 BOR-BR, BOR-SB, MLY-PM.
8.2. *Miquelia celebica* Blume
Distribution: 42 BOR-BR, BOR-SB, BOR-SR, PHI, SUL, SUM.
8.3. *Miquelia philippinensis* Merr.
Distribution: 42 PHI.
8.4. *Miquelia reticulata* Merr.
Distribution: 42 PHI.

9. *Nothapodytes* Blume
9.1. *Nothapodytes foetida* (Wight) Sleumer
Distribution: 42 PHI, SUM.
9.2. *Nothapodytes montana* Blume
Distribution: 42 JAW, LSI-LS, SUM.

10. *Phytocrene* Wall.
10.1. *Phytocrene anomala* Merr.
Distribution: 42 BOR-SB, BOR-SR.
10.2. *Phytocrene borneensis* Becc.
Distribution: 42 BOR-BR, BOR-KA, BOR-SB.
10.3. *Phytocrene bracteata* Wall.
Distribution: 42 BOR-BR, BOR-KA, BOR-SB, BOR-SR, MLY-PM, SUM.
10.4. *Phytocrene hirsuta* Blume
Distribution: 42 MOL, SUL.
10.5. *Phytocrene interrupta* Sleumer
Distribution: 43 NWG-PN.
10.6.1. *Phytocrene macrophylla* Blume var. *macrophylla*
Distribution: 42 JAW, PHI, SUM.
10.6.2. *Phytocrene macrophylla* Blume var. *caudigera* (Sleumer) Sleumer
Distribution: 42 BOR-SB.
10.6.3. *Phytocrene macrophylla* Blume var. *dasycarpa* (Miq.) Sleumer
Distribution: 42 SUL.
10.7. *Phytocrene malacothrix* Sleumer
Distribution: 43 NWG-PN.
10.8. *Phytocrene oblonga* Wall.
Distribution: 42 MLY-PM.
10.9. *Phytocrene palmata* Wall.
Distribution: 42 MLY-PM, SUM.
10.10. *Phytocrene racemosa* Sleumer
Distribution: 42 BOR-SR.
10.11. *Phytocrene trichura* Ridl.
Distribution: 42 MLY-PM.

11. *Platea* Blume
11.1. *Platea bullata* Sleumer
Distribution: 42 BOR-SR.
11.2.1. *Platea excelsa* Blume var. *excelsa*
Distribution: 42 JAW, SUM.
11.2.2. *Platea excelsa* Blume var. *riedeliana* (Becc.) Sleumer
Distribution: 42 BOR-BR, BOR-SB, BOR-SR, MLY-PM, MLY-SI, SUM.
11.2.3. *Platea excelsa* Blume var. *microphylla* (Sleumer) Sleumer
Distribution: 43 NWG-IJ, NWG-PN.
11.2.4. *Platea excelsa* Blume var. *borneensis* (Heine) Sleumer
Distribution: 42 BOR-BR, BOR-SB, BOR-SR, JAW, LSI-BA, LSI-LS, MOL, MLY-PM, MLY-SI, PHI, SUL, SUM; 43 BIS, NWG-IJ, NWG-PN.
11.2.5. *Platea excelsa* Blume var. *kinabaluensis* (Sleumer) Sleumer
Distribution: 42 BOR-SB.
11.3. *Platea latifolia* Blume
Distribution: 42 BOR-BR, BOR-KA, BOR-SB, BOR-SR, JAW, MLY-PM, MLY-SI, PHI, SUL, SUM; 43 BIS, NWG-IJ, NWG-PN.
11.4. *Platea malayana* Utteridge
Distribution: MLY-PM.
11.5. *Platea sclerophylla* Sleumer
Distribution: 42 BOR-SB.

12. *Polyporandra* Becc.
12.1. *Polyporandra scandens* Becc.
Distribution: 42 MOL; 43 NWG-IJ, NWG-PN, SOL-NO, SOL-SO.

13. *Pyrenacantha* Wight
13.1. *Pyrenacantha repanda* (Merr.) Merr.
Distribution: 42 PHI.

14. *Rhyticaryum* Becc.
14.1. *Rhyticaryum elegans* G.Schellenb.
Distribution: 43 NWG-IJ, NWG-PN.
14.2. *Rhyticaryum fasciculatum* Becc.
Distribution: 43 NWG-IJ.
14.3. *Rhyticaryum gracile* G.Schellenb.
Distribution: 43 NWG-PN.
14.4. *Rhyticaryum longifolium* K.Schum. & Lauterb.
Distribution: 43 NWG-IJ, NWG-PN.
14.5. *Rhyticaryum lucidum* G.Schellenb.
Distribution: 43 NWG-PN.
14.6. *Rhyticaryum macrocarpum* Becc.
Distribution: 43 NWG-IJ, NWG-PN.

14.7. *Rhyticaryum novoguineense* (Warb.) Sleumer
Distribution: 43 NWG-PN.
14.8. *Rhyticaryum oleraceum* Becc.
Distribution: 42 LSI-LS, MOL; 43 NWG-IJ.
14.9. *Rhyticaryum oxycarpum* K.Schum. & Lauterb.
Distribution: 43 NWG-PN.
14.10. *Rhyticaryum purpurascens* G.Schellenb.
Distribution: 43 NWG-PN.
14.11. *Rhyticaryum racemosum* Becc.
Distribution: 43 NWG-IJ.
14.12. *Rhyticaryum rotundatum* G.Schellenb.
Distribution: 43 NWG-PN.

15. *Sarcostigma* Wight & Arn.
15.1. *Sarcostigma kleinii* Wight & Arn.
Distribution: 42 BOR-SR, JAW, MLY-PM.
15.2. *Sarcostigma paniculata* Pierre
Distribution: 42 BOR-BR, BOR-SR, MLY-PM, PHI.

16. *Sleumeria* Utteridge, Nagam. & Teo
16.1. *Sleumeria auriculata* Utteridge, Nagam. & Teo
Distribution: 42 BOR-BR, BOR-KA, BOR-SB, BOR-SR.

STEMONURACEAE

Members of Stemonuraceae are trees or shrubs with falcate, naked terminal buds, entire alternate leaves, and usually green young twigs. Inflorescences may be axillary, terminal or leaf-opposed (rarely ramiflorous), with one to many flowers, often umbelliform with cymose branches. The flowers are bisexual or functionally unisexual, with a small cupular calyx and 4–5 free to connate petals that are often inflexed at the apex. The stamens (and staminodes) are characteristically flattened (except *Codiocarpus*), with clavate hairs on the filament. The fruits are usually white, yellow, pink or red, and three genera have a prominent lateral appendage on one side of the drupe. Recently *Gomphandra* and *Medusanthera* have been revised with new species described (see Schori 2010, Schori & Utteridge 2010, and Utteridge 2011), and a new species of *Stemonurus* has been described (Utteridge & Schori 2009).

17. *Cantleya* Ridl.
17.1. *Cantleya corniculata* (Becc.) R.A.Howard
Distribution: 42 BOR-BR, BOR-KA, BOR-SB, BOR-SR, MLY-PM, MLY-SI, SUM.

18. *Codiocarpus* R.A.Howard
18.1. *Codiocarpus merrittii* (Merr.) R.A.Howard
Distribution: 42 PHI.

19. *Gomphandra* Wall. ex Lindl.

19.1. *Gomphandra angustata* Schori ined.
Distribution: 43 NWG-PN.
19.2. *Gomphandra australiana* F.Muell.
Distribution: 42 MOL; 43 NWG-PN.
19.3. *Gomphandra borneensis* Schori ined.
Distribution: 42 BOR-BR, BOR-SB, BOR-SR.
19.4. *Gomphandra bracteata* Schori ined.
Distribution: 42 PHI.
19.5. *Gomphandra capitulata* (Jungh. & de Vriese) Becc.
Distribution: 42 BOR-KA, MLY-PM, SUM.
19.6. *Gomphandra coi* Schori ined.
Distribution: 42 PHI.
19.7. *Gomphandra chimaera* Schori ined.
Distribution: 42 SUM.
19.8. *Gomphandra conklinii* Schori
Distribution: 42 PHI.
19.9. *Gomphandra cumingiana* (Miers) Fern.-Vill.
Distribution: 42 BOR-KA, BOR-SB, BOR-SR, PHI.
19.10. *Gomphandra dinagatensis* Schori ined.
Distribution: 42 PHI.
19.11. *Gomphandra dolichocarpa* Merr.
Distribution: 42 SUM.
19.12. *Gomphandra engganensis* Schori ined.
Distribution: 42 SUM.
19.13. *Gomphandra fernandoi* Schori & Utteridge ined.
Distribution: 42 PHI.
19.14. *Gomphandra flavicarpa* (Elmer) Merr.
Distribution: 42 PHI.
19.15. *Gomphandra fuliginea* (Elmer) Merr.
Distribution: 42 PHI.
19.16. *Gomphandra fusiformis* Sleumer
Distribution: 42 SUM.
19.17. *Gomphandra halconensis* Schori
Distribution: 42 PHI.
19.18. *Gomphandra jacobsii* Schori ined.
Distribution: 42 SUM.
19.20.1. *Gomphandra javanica* (Blume) Valeton subsp. *javanica*
Distribution: 42 JAW, LSI-BA, LSI-LS.
19.20.2. *Gomphandra javanica* (Blume) Valeton subsp. *pseudojavanica* (Sleumer) Schori ined.
Distribution: 42 SUM.
19.21.1. *Gomphandra kinabaluensis* Schori ined. var. *kinabaluensis*
Distribution: 42 BOR-SB.

19.21.2. *Gomphandra kinabaluensis* Schori var. *clemensiorum* Schori ined.
Distribution: 42 BOR-SB.
19.22. *Gomphandra lamanii* Schori ined.
Distribution: 42 BOR-KA, BOR-SR.
19.23. *Gomphandra lancifolia* Merr.
Distribution: 42 PHI.
19.24. *Gomphandra longipedunculata* Schori ined.
Distribution: 42 BOR-SR.
19.25.1. *Gomphandra luzoniensis* (Merr.) Merr. subsp. *luzoniensis*
Distribution: 42 PHI.
19.25.2. *Gomphandra luzoniensis* (Merr.) Merr. subsp. *septentrionalis* Schori & Utteridge ined.
Distribution: 38 TAI; 42 PHI.
19.26. *Gomphandra lysipetala* Stapf
Distribution: 42 BOR-SB, BOR-SR.
19.27. *Gomphandra macrosperma* Schori ined.
Distribution: 42 BOR-SB.
19.28. *Gomphandra mappioides* Valeton
Distribution: 42 LSI-ET, LSI-LS, MOL, PHI, SUL.
19.29.1. *Gomphandra melanesiensis* Schori ined. subsp. *melanesiensis*
Distribution: 43 BIS, SOL-NO, SOL-SO.
19.29.2. *Gomphandra melanesiensis* Schori subsp. *macrocarpa* Schori ined.
Distribution: 43 SOL-SO.
19.30. *Gomphandra microcarpa* Schori ined.
Distribution: 42 MLY-PM.
19.31. *Gomphandra montana* (G. Schellenb.) Sleumer
Distribution: 43 NWG-PN.
19.32. *Gomphandra muscosa* Schori ined.
Distribution: 43 NWG-PN.
19.33. *Gomphandra oblongifolia* Merr.
Distribution: 42 PHI.
19.34. *Gomphandra oligantha* Sleumer
Distribution: 42 PHI.
19.35. *Gomphandra palustris* Schori
Distribution: 42 BOR-SR.
19.36. *Gomphandra papuana* (Becc.) Sleumer
Distribution: 43 NWG-IJ, NWG-PN.
19.37.1. *Gomphandra parviflora* (Blume) Valeton var. *parviflora*
Distribution: 42 SUM.
19.37.2. *Gomphandra parviflora* (Blume) Valeton var. *magnifolia* Schori ined.
Distribution: 42 SUM.
19.37.3. *Gomphandra parviflora* (Blume) Valeton var. *paucibarbata* Schori ined.
Distribution: 42 SUM.

19.38. *Gomphandra psilandra* Schori ined.
Distribution: 42 PHI.
19.39. *Gomphandra pseudoprasina* Sleumer
Distribution: 43 NWG-PN.
19.40. *Gomphandra puberula* Ridl.
Distribution: 42 MLY-PM.
19.41. *Gomphandra quadrifida* (Blume) Sleumer
Distribution: 42 MLY-PM, MLY-SI, SUM.
19.42. *Gomphandra ramuensis* (Lauterb.) Sleumer
Distribution: 43 NWG-IJ, NWG-PN.
19.43. *Gomphandra rarinervis* Schori
Distribution: 43 NWG-PN.
19.44. *Gomphandra schoepfiifolia* Sleumer
Distribution: 43 NWG-PN.
19.45. *Gomphandra simalurensis* Sleumer
Distribution: 42 SUM.
19.46. *Gomphandra simulans* Schori ined.
Distribution: 42 SUM.
19.47. *Gomphandra subcordata* Schori ined.
Distribution: 43 NWG-PN.
19.48. *Gomphandra subrostrata* Merr.
Distribution: 42 SUM.
19.49. *Gomphandra tenuis* Schori ined.
Distribution: 42 MLY-PM.
19.50. *Gomphandra tomentella* (Kurz) Mast.
Distribution: 41 THA; 42 MLY-PM.
19.51. *Gomphandra ultramafiterrestris* Schori ined.
Distribution: 42 PHI.
19.52. *Gomphandra velutina* Sleumer
Distribution: 42 SUL.

20. *Hartleya* Sleumer
20.1. *Hartleya inopinata* Sleumer
Distribution: 43 NWG-PN.

21. *Medusanthera* Seem.
21.1. *Medusanthera gracilis* (King) Sleumer
Distribution: 42 MLY-PM, SUM.
21.2. *Medusanthera inaequalis* Utteridge
Distribution: 43 NWG-IJ.
21.3. *Medusanthera laxiflora* (Miers) R.A.Howard
Distribution: 42 PHI; 43 NWG-IJ, NWG-PN, SOL-NO, SOL-SO.
21.4. *Medusanthera malayana* Utteridge
Distribution: 42 MLY-PM.

21.5. *Medusanthera megistocarpa* Utteridge
Distribution: 43 NWG-PN.

22. *Stemonurus* Blume
22.1. *Stemonurus ammui* (Kaneh.) Sleumer
Distribution: 43 BIS, NWG-PN, NWG-IJ, SOL-NO, SOL-SO.
22.2. *Stemonurus celebicus* Valeton
Distribution: 42 SUL.
22.3. *Stemonurus corrugatus* Utteridge & Schori
Distribution: 42 BOR-SR.
22.4. *Stemonurus gitingensis* (Elmer) Sleumer
Distribution: 42 PHI.
22.5. *Stemonurus grandifolius* Becc.
Distribution: 42 BOR-SB, BOR-SR, BOR-KA.
22.6. *Stemonurus hallieri* (Merr.) Merr.
Distribution: 42 PHI.
22.7. *Stemonurus malaccensis* (Mast.) Sleumer
Distribution: 42 BOR-KA, BOR-SB, BOR-SR, BOR-BR, MLY-PM.
22.8. *Stemonurus monticola* (G. Schellenb.) Sleumer
Distribution: 43 NWG-IJ, NWG-PN.
22.9. *Stemonurus scorpioides* Becc.
Distribution: 42 BOR-BR, BOR-SB, BOR-SR, JAW, MLY-PM, MLY-SI, SUM.
22.10. *Stemonurus secundiflorus* Blume
Distribution: 42 BOR-BR, BOR-KA, BOR-SB, BOR-SR, JAW, MLY-PM, SUM.
22.11. *Stemonurus umbellatus* Becc.
Distribution: 42 BOR-SR, BOR-KA, BOR-BR, BOR-SB, MLY-PM.

23. *Whitmorea* Sleumer
23.1. *Whitmorea grandiflora* Sleumer
Distribution: 43 SOL-NO, SOL-SO.

Summary

Family changes due to molecular and morphological data have altered the concept of many families in the Flora Malesiana region. These family changes are summarised in the APG publications (e.g., see Stevens 2001). The Icacinaceae is one such family and has now been re-circumscribed into new groups. In 1971 the family was published for the Flora Malesiana and, with the Cardiopteridaceae considered a separate family, the group then included 100 species in 22 genera in two families (Sleumer 1971a, 1971b). The current concept of the group is now of three families: Icacinaceae s.str. with 48 species in 12 genera; Cardiopteridaceae with 15 species in four genera; and Stemonuraceae with 72 species in seven genera.

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Clerodendrum confusion—redefinition of, and new perspectives for, a large Labiate genus

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ABSTRACT. Formerly referred to Verbenaceae s.l., *Clerodendrum* L. is one of the largest genera within the Lamiaceae (Labiatae) s.l., and many of its species are of ecological and commercial importance. However, confusion about species delimitation and identification has reigned for many decades, resulting in large quantities of unidentified, or misidentified, herbarium material. Results from recent molecular studies have provided a framework for accurate placement of taxa. The revised concept of the genus is applied to taxa in Malesia in order to produce a modern account for Flora Malesiana, which includes up-to-date descriptions and much-needed keys. Progress made so far is reported.

Keywords. *Clerodendrum*, Labiatae, Lamiaceae, Malesia, Verbenaceae s.l.

Introduction

The long-standing Flora Malesiana project, first and foremost, aims to create "a systematic account of the flora of Malesia, the plant-geographical unit spanning six countries in Southeast Asia" (www.floramalesiana.org). With such high botanical diversity in the region (an estimated 42,000 plant species: Roos 1993) and general paucity of funds for research, why is *Clerodendrum* a genus worthy of particular note?

Clerodendrum is a large genus containing species that are important both ecologically and commercially. The ecology of, often genus-specific, associations with microfungi (Hosagoudar & Archana 2009, and see Minter 2010), and relationships with ants (Maschwitz et al. 1994) and pollinators (Corner 1940, Yuan et al. 2010) has been studied to a limited extent though further research is required in order to understand these complex interactions. Some species are early successional colonisers of degraded land (e.g., *C. japonicum* (Thunb.) Sweet) and could be used for habitat restoration, but, others, like *C. chinense* (Osbeck) Mabb., can become pernicious weeds, so that accurate identification and careful consideration must go hand-in-hand before implementing restoration work. Many of the Malesian and other species are highly ornamental, having large showy inflorescences and attractive foliage, and some are already popular in the global horticultural trade (several, including the spectacular orangey red and cream to pale yellow-flowered forms of *C. paniculatum* L., can be

Fig. 1. Two colour forms of *Clerodendrum paniculatum* are popular in cultivation due to their striking inflorescences and foliage (one form has cream to pale yellow corollas with green inflorescence branches, and the other has pale orangey-red corollas with red inflorescence branches). These plants are growing in the Singapore Botanic Gardens. Photos by J.A. Wearn, 2010.

seen in the Singapore Botanic Gardens, for example; see Fig. 1). *Clerodendrum* species have also been used medicinally for centuries in their countries of origin and rigorous scientific trials are now underway to evaluate the potential of compounds extracted from them, notably those with antipyretic and anti-inflammatory properties (examples are cited in Shrivastava & Patel 2007), and antiviral activity (Kim et al. 2001).

Clerodendrum was long referred to Verbenaceae s.l. but its placement was corrected following a series of molecular-based studies (Olmstead et al. 1993, Wagstaff et al. 1998), such that it now falls into Lamiaceae (Labiatae). Molecular studies during the 1990s lacked resolution below family level as only a few species from each of the constituent genera were included. Although previously considered as a pantropical and eastern temperate genus, it was recognised that *Clerodendrum* in this broad sense was heterogenous and likely to be polyphyletic. The need for elucidation of inter- and intrageneric relationships was addressed in a landmark paper by Yuan et al. (2010), using cpDNA from 56 taxa (including 40 *Clerodendrum* species, *sensu* Steane et al. 2004). They showed that the native American species were misplaced in *Clerodendrum* and so those are now referred to other genera. Many of the African taxa had already been excluded and placed in a revived *Rotheca* Raf., a more distantly allied genus (Steane & Mabberley 1998, Steane et al. 2004). A combination of molecular and morphological taxonomic studies necessitated reassessment of traditionally used morphological characters, allowing the focus to be directed towards those characters now seen as most relevant for taxonomic delimitation at the generic level and below. Thus, a redefinition of *Clerodendrum* s.s. and its allies was completed (Yuan et al. 2010). This allowed us to undertake a reassessment of all Malesian taxa, previously considered to be '*Clerodendrum*'.

Towards a reassessment of Malesian taxa

When Moldenke (1985: 310) wrote of *Clerodendrum sensu lato*, he referred to 584 taxa, the majority of which had one or more synonyms. Now numbering approximately 150–180 species, *Clerodendrum* is an exclusively Old World genus, its species distributed largely within the tropics and subtropics with some found as far south as Australia and as far north as central China and Japan. Outside Africa, the majority of *Clerodendrum* species is found in the Malesian region but there has been no major revisionary work on those for nearly a century. Thus, at the outset, we were largely reliant upon the accounts of Schauer (1847) and Lam (1919). An account by Backer & Bakhuizen van den Brink (1965) included taxa found in Java while a series of later papers (Moldenke 1985–87) covered the genus only in part, with some questionable infraspecific delimitation and other circumscriptions. One of us (DM) had prepared a manuscript account of the genus and its allies for the Flora of Peninsular Malaysia (Mabberley, in press) but it became obvious very quickly, from the literature alone, that there were a multitude of names in use and abundant synonymy (varying depending on the author) applied to taxa beyond the Malay Peninsula. However, it was not until one of us (JW) began to trawl through the large numbers unidentified or misnamed collections in herbaria that the confusion of species concepts and the full extent of the task were realised. It was not uncommon for material to have been reidentified several times—in some cases reaching a nomenclatural 'full circle', where the last botanist viewing a particular collection had disagreed with those before him/her but agreed with the original, contemporary identification! It soon became apparent that the Flora Malesiana account would require a revision of monographic intensity.

Flora Malesiana and the future of *Clerodendrum*

As we near the end of our reassessment of *Clerodendrum* in Malesia, 210 names have been considered since our project began in mid-2008 (Wearn & Mabberley, in prep.). So far, 53 species are recognised, 13 names have been excluded from the genus (referred to *Faradaya* F. Muell., *Hosea* Ridl., *Rotheca* and *Volkameria* L.) and two have been excluded from the *Flora Malesiana* account due to incorrect understanding of distributions (species now thought to be native or naturalised only outside Malesia). A further eight names remain 'insufficiently known'. The loss of type material and lack of other collections aligning with the descriptions has meant that no progress in such cases can yet be made. For example, *Clerodendrum barba-felis* Hallier f. was described based on material deposited at WRSL, with a duplicate at PNH, now both lost, with no conspecific material found elsewhere. This situation is by no means peculiar to *Clerodendrum* as nearly every volume of Flora Malesiana contains names excluded from accounts in this way. Unfortunately, it is a geographically and taxonomically wide-ranging phenomenon, owed in part to the destruction of herbaria or loss of sets through auctions, fires and so on, but perhaps also through the rarity of the species described. Considering the rate of destruction of habitats in Malesia, the species that have not been collected for over 50 years may now be extinct, particularly as *Clerodendrum* species are by no means cryptic.

While many *Clerodendrum* species are not considered of conservation concern, being commonly collected (e.g., *C. disparifolium* Blume), several have not been seen in Malesia for 50 years or more (e.g., *C. umbratile* King & Gamble (Mabberley, in press)), whether due to geographical sampling effort or species rarity. A few species have very restricted geographical ranges and are considered vulnerable (e.g., *C. lankawiense* King & Gamble, which is found only on certain islands off south-west Peninsular Thailand and northwest Peninsular Malaysia (Mabberley, in press)). Others, such as *C. albiflos* H.J. Lam from New Guinea and *C. multibracteatum* Merr. from the Philippines, are known from only one or a few collections, and so have to be categorised as 'data deficient' until more is known. Unfortunately, but perhaps not surprisingly, the species that are in cultivation are those which are common naturally, perhaps due as much to the ease with which they can be propagated and grown as it is a result of their floral appeal. Currently, there is no *ex situ* conservation resource.

Plants of the genus are commonly encountered during fieldwork but frequently unidentified, or worse, misidentified so that they end up in completely the wrong herbarium cupboard. We hope that our work for Flora Malesiana will clarify the seemingly ubiquitous confusion which has dominated this large and important genus for so long because our revision of Malesian *Clerodendrum* taxa has allowed preparation of new descriptions and keys (Wearn & Mabberley, in press, in prep.), which are a prerequisite for accurate identification in the field and herbarium. These will aid taxonomists as well as those undertaking conservation and restoration work.

In conclusion, the importance of interdisciplinary collaboration (such as between taxonomists, ethnobotanists and ecologists) and knowledge exchange must be emphasised, as through this process much more can be understood about the taxa we study. Indeed, the information that one seeks may have been already documented, but until experts in other disciplines are consulted, no-one may be able to make full use of the incomplete knowledge. For example, during this work, JW found that *C. rumphianum* de Vriese & Teijsm., described from Ambon in Indonesia, was poorly known by taxonomic botanists. An adequate account of the plant was created only as a result of contact with an ethnobotanist (Roy Ellen at the University of Kent). RE had encountered the plant several times during long-term (1970–present) research on the neighbouring island of Seram and was able to provide much additional information including photographs and notes on local uses, in addition to much-needed recent material (Wearn & Ellen, in prep.).

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A synopsis of *Coelostegia* (Bombacaceae/Malvaceae: Helicteroideae: Durioneae) and new records from Borneo

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ABSTRACT. A synoptic revision of *Coelostegia* Benth. (Bombacaceae/Malvaceae subfam. Helicteroideae–Durioneae) in Borneo is given. Six species are recognised, of which four (*C. chartacea*, *C. kostermansii*, *C. montana* and *C. neesiocarpa*) are endemic to Borneo. *Coelostegia griffithii*, previously recorded only from Peninsular Malaysia, Singapore, Java and Sumatra, is now also found in Borneo, while *C. montana* previously known only from Sarawak and Kalimantan also occurs in Sabah. Gross morphological and micromorphological characters show that the genus *Coelostegia* can be readily distinguished from other genera in the Durioneae-group by the epicalyx being much shorter than the calyx, the induplicate-saccate calyx character and the ovary being partly enclosed by the receptacle. The distinction is also supported by micromorphological characters derived from trichomes, stomata, and pollen. Nomenclatural (typification and synonymy) and taxonomic notes, ecology and geographical distribution of the recognised species are provided.

Keywords. Borneo, *Coelostegia*, Durioneae, Helicteroideae, Malvaceae, taxonomy

Introduction

Bentham (1862) first described *Coelostegia* with one species, *C. griffithii*, from Peninsular Malaysia. Beccari (1886) described two more species, from Sumatra (*C. sumatrana*) and Borneo (*C. borneensis*), and was the first to describe the fruit and seed of *Coelostegia*. Soegeng (1960) revised the genus and added three more species from Borneo, and provided full descriptions, an identification key and illustrations of all five species known to him. Sidiyasa (2001) described a new species, *C. montana*, from East Kalimantan and Sarawak.

Prior to 1998, taxonomic and systematic studies based mainly on morphological and anatomy characters carried out by various authors (e.g., Hutchinson 1959; Cronquist 1968, 1981; Keng 1969; Takhtajan 1969) included *Boschia*, *Coelostegia*, *Cullenia*, *Durio*, *Kostermansia* and *Neesia* in the tribe section Durioneae of the family Bombacaceae. From the late 1990's, however, phylogenetic studies based on chloroplast and nuclear ribosomal DNA (e.g., Alverson et al. 1998, 1999; Baum et al. 1998; Bayer et al. 1999; Nyffeler & Baum 2000; Bayer & Kubitzki 2003) strongly suggested that the core Malvales families (Bombacaceae, Malvaceae, Sterculiaceae and Tiliaceae) should be merged into an expanded family Malvaceae, and that nine subfamilies should be recognised, with the genera of the Durioneae-group to be included in subfam. Helicteroideae-Durioneae. Cheek (2006, 2007), however, disagreed and proposed placing the Durioneae genera in a separate family, the Durionaceae.

Synopsis of recognised taxa

Coelostegia Benth., Gen. Pl. 1 (1862) 213; Hooker f., Fl. Brit. India 1 (1875) 352; Beccari, Malesia 3 (1889) 269; King, J. As. Soc. Beng. 60, 1 (1891) 56; Schumann in Engler & Prantl., Nat. Pflanzenfam. 3, 6 (1895) 68; Ridley, Fl. Malay Penins. 1 (1922) 266; Bakhuizen f., Bull. Jard. Bot. Buitenz. 6, 3 (1924) 223; Soegeng, Reinwardtia 5, 3 (1960) 270; Hutchinson, Gen. Flow. Pl. 2 (1967) 526; Kochummen, Tree Fl. Malaya 1 (1972) 104; Cockburn, Trees of Sabah 1 (1976) 22; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 53; Salma et al., Pl. Resources of South-East Asia 5, 2 (1995) 140; Coode et al. (eds), Checkl. Flow. Pl. Gymno. Brunei (1996) 41; Argent et al. (eds), Man. Non-Dipt. Trees Centr. Kalimantan 1 (1997) 96; Beaman et al., Pl. Mount Kinabalu 4 (2001) 164; Bayer & Kubitzki, Fam. Gen. Vasc. Pl. 5 (2003) 261. TYPE SPECIES: *Coelostegia griffithii* Benth.

Distribution. Six species distributed in Sumatra (including Riau Archipelago), Peninsular Malaysia, Java, Singapore and Borneo. In Borneo, four species are endemics; Sarawak has five species (non endemic); Sabah three species (non endemic); Brunei two species (non endemic) and Kalimantan five species (one endemic) (Fig 1).

Ecology. Lowland mixed dipterocarp and lower montane forest on clay-rich soils, to c. 1450 m.

Notes. Soegeng (1959, 1960) pointed out that based on their overall vegetative and reproductive characters, *Coelostegia, Durio, Kostermansia* and *Neesia* are distinct genera but closely related to one another. Basing his conclusion on the anatomy of vegetative parts, Baas (1972) fully supported Soegeng's suggestion. Appendix A summarises the macromorphological and micromorphological characters which can be used to distinguish *Coelostegia* from the other genera.

1. *Coelostegia borneensis* Becc., Malesia 3 (1889) 272, Nelle Foreste Di Borneo (1902) 572; Merrill, J. Str. Br. Roy. As. Soc., Spec. No. (1921) 377; Bakhuizen f., Bull. Jard. Bot. Buitenz. 6, 3 (1924) 224; Masamune, En. Phan. Born. (1942) 454; Soegeng, Reinwardtia 5, 3 (1960) 272; Kochummen, Tree Fl. Malaya 1 (1972) 106; Anderson, Checkl. Trees Sarawak (1980) 153; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 54; Turner, Gard. Bull. Sing. 47, 1 (1995) 151; Salma et al., Pl. Resources of South-East Asia 5, 2 (1995) 143; Argent et al. (eds), Man. Non-Dipt. Trees Centr. Kalimantan 1 (1997) 97. TYPE: *Beccari PB 2688,* Borneo, Sarawak, Kuching district (holo FI, iso BO! K!).

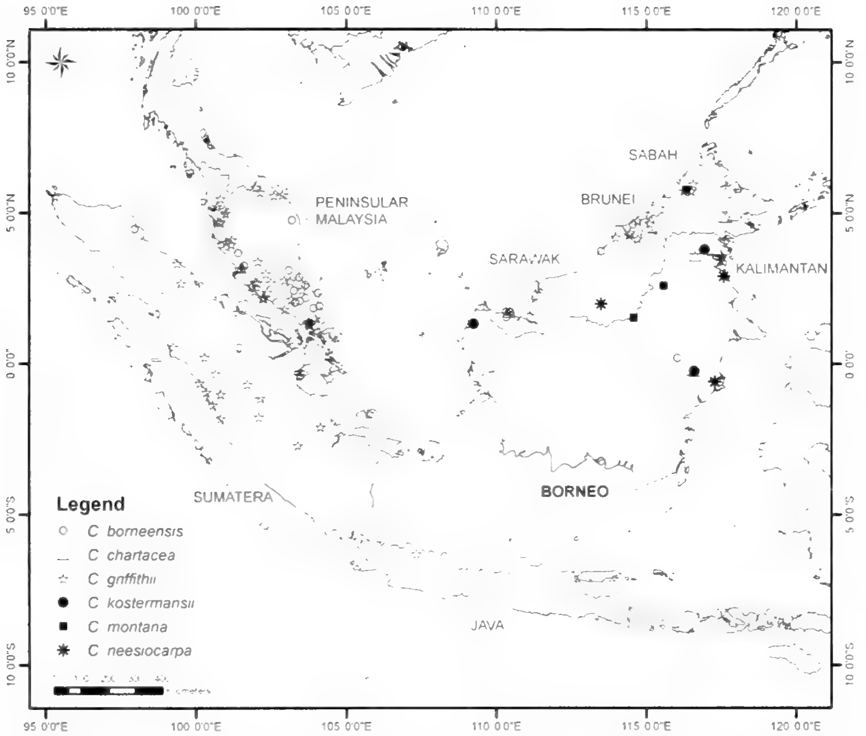

Fig. 1. Distribution of six *Coelostegia* species in Peninsular Malaysia, Singapore, Borneo, Sumatra and Java.

Distribution. Sumatra, Peninsular Malaysia and Borneo (Sarawak, Kalimantan, Brunei).

Ecology. Lowland mixed dipterocarp, *kerangas* and swampy forest on slopes, river banks, hillsides, low undulating country, on waterlogged soils and deep yellow sands overlying tertiary clays at altitude 20–303 m.

Notes. In leaf surface, size, number of lateral veins, twig and types of fruit spines, *C. borneensis* is closely related to *C. chartacea* but differs in the leaf texture (coriaceous vs. chartaceous), leaf apex (short-acuminate, acumen 0.6 cm vs. long-acuminate, acumen up to 1.5 cm), and fruit shape (globular vs. ellipsoid).

Specimens examined: PENINSULAR MALAYSIA. **Johor**: Lenggor FR, *Whitmore FRI 8651* (KEP); Gunung Sumalayang, *Everett FRI 13875* (K, KEP, L, SAN, SING); Panti FR, *Pilus KEP 104507* (KEP); Labis FR, *Yaacob KEP 104744* (KEP); Kluang FR, *Heaslett s.n.* (KEP); ibid., *Samsuri SA 391* (SING); Kg. Hubong, *Kadim KN 284* (BO, L, SING). **Pahang**: Aur FR, *Whitmore FRI 3626* (KEP, L); Kuala Kemapan, *Saw FRI 34187* (KEP); Menchali FR, *Meijer KEP 94890* (K, KEP, L, SING). **Selangor**: Bukit Lagong FR, *Hamid KEP 81089* (KEP); Bukit Belata FR, *Kochummen KEP 99372* (KEP); **Terengganu**: Dungun, *Abdullah KEP 53363* (BO, KEP). – SUMATRA. **North**

Sumatra: Langsa, *Boschbouwproefstation bb. 2578* (BO, BZF, L). **East Sumatra**: Pakan Baru, Tenajan River, *Soepadmo 252* (BO). – BORNEO. **Sarawak**: Bako NP, *Yap 527* (KEP); ibid., *Ashton S 24320* (A, BO, K, L, SAN, SAR, SING); ibid., *Kuswata 401* (BO, K, L, SING); Similajau FR, *Brunig S 8631* (BO, L, SAN); Telok Belian, *Ilias Paie S 35997* (KEP, L); Kuching, *Beccari PB 2688* (BO, K) (type). **Brunei**: Andulau FR, *Ashton BRUN 586* (KEP, L, SING). **Kalimantan**: East Kalimantan, Ulu Mahakam, *Sidiyasa 1653* (BO, KEP, L, SAN, WAN). Central Kalimantan, Sampit River, near Kuala Kuajan, *Kostermans 8070* (BO).

2. *Coelostegia chartacea* Soegeng, Reinwardtia 5, 3 (1960) 273; Argent et al. (eds), Man. Non-Dipt. Trees Centr. Kalimantan 1 (1997) 97. TYPE: *Kostermans 5262*, Indonesia, East Kalimantan, East Kutei, Sangkulirang, Menubar R. (holo BO! iso A, K, L! LAE, P, PNH, SING!).

Distribution. Endemic in Borneo (Sabah, Sarawak, Kalimantan).

Ecology. In primary forest, on hill and riversides at 25–606 m altitude.

Notes. A very distinct species that can be distinguished from the other species of *Coelostegia* by its chartaceous leaves. Morphologically, *C. chartacea* is closely related to *C. borneensis* but differs in its longer leaf acumen and the ellipsoid fruit (see note on *C. borneensis*).

Specimens examined: BORNEO. **Sabah**: Lung Manis FR, *Charington SAN 24731* (K, SAN); Tankong, *Lassan SAN 72805* (SAN); Sungai Beatrice, *Cockburn SAN 84979* (K, SAN); Sungai Bole, *Lee SAN 96767* (SAN); Ulu Segama, *Tamin SAN 98872* (SAN). **Sarawak**: Samunsam Wildlife Sanctuary, *Abang Mohtar S 52657* (KEP, SAR); Bako NP, *Nadiah et al. S 100582* (KEP). **Kalimantan**: East Kalimantan, Desa Gong Solok, *Arifin AA 3010* (BO, WAN); Sungai Menubar, *Kostermans 5262* (BO, L, SING) (type); Belajan River near Tabang, *Kostermans 10679* (K); Tidoengsche Landen, *bb. 17958* (BO, BZF, L).

3. *Coelostegia griffithii* Benth., Gen. Pl. 1 (1862) 213; Hooker f., Fl. Brit. India 1 (1875) 353; Masters, J. Linn. Soc. Bot. 14 (1875) 505; Beccari, Malesia 3 (1889) 270; King, J. As. Soc. Beng. 60, 1 (1891) 57; Schumann in Engler & Prantl., Nat. Pflanzenfam. 3, 6 (1895) 68; Ridley, Fl. Malay Penins. 1 (1922) 266; Bakhuizen f., Bull. Jard. Bot. Buitenz. 6, 3 (1924) 224; Soegeng, Reinwardtia 5, 3 (1960) 274; Kochummen, Tree Fl. Malaya 1 (1972) 106; Cockburn, Trees of Sabah 1 (1976) 23; Anderson, Checkl. Trees Sarawak (1980) 153; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 54; Turner, Gard. Bull. Sing. 47, 1 (1995) 151; Coode et al. (eds), Checkl. Flow. Pl. Gymno. Brunei (1996) 41; Beaman et al., Pl. Mount Kinabalu 4 (2001) 164. TYPE: *Griffith 547*, Malaya, Malacca (holo K! iso A, L! P).

Coelostegia sumatrana Becc., Malesia 3 (1889) 271; Bakhuizen f., Bull. Jard. Bot. Buitenz. 6, 3 (1924) 224; *Coelostegia griffithii* Benth. forma *sumatrana* (Becc.) Bakhuizen f., Bull. Jard. Bot. Buitenz. 6, 3 (1924) 248. TYPE: *Beccari PS 738*, West Sumatra, Padang Prov., Air Manchur (holo FI, iso BO! K! L!).

Distribution. Sumatra (including Riau Archipelago), Peninsular Malaysia, Singapore, Java and Borneo (Sabah, Sarawak, Brunei) (Fig. 1).

Ecology. In mixed dipterocarp, *kerangas* and lower montane forests at 15–1393 m.

Notes. Soegeng (1960) cited *C. griffithii* as occurring only in Peninsular Malaysia, Sumatra and Bangka. Detailed comparative study of specimens currently available at BO, K, L, SAN and SAR herbaria show that the species also occurs in Borneo.

In Borneo, sterile specimens of *C. griffithii* can be easily confused with those of *C. kostermansii, C. neesiocarpa* and *C. montana*. However, the fruit surface of *C. griffithii* is typically covered with sharp conical spines compared to that of the other three species which have a smooth or submuricate or muricate surface.

Specimens examined (* denotes new records in Borneo; ** denotes additional localities in Peninsular Malaysia): PENINSULAR MALAYSIA. **Johor**: Bukit Paloh Estate, *Mohd Shah MS 395* (BO, SAR, SING); Labis FR, *Whitmore FRI 3847* (KEP); Banang FR, *Suleiman KEP 70172* (KEP). ****Kedah**: Gunung Inas FR, *Whitmore FRI 4694* (KEP). **Kelantan**: Kemahang FR, *Chelliah FRI 6502* (K, KEP, L); Kuala Balak, *Suppiah FRI 28017* (K, KEP, L); Temangan, *Baki KEP 68766* (KEP). **Malacca**: loc. not. indicated, *Derry 123* (SING); ibid., *Griffith 547* (K, L) (type); Bukit China, *Derry 95* (SING); Selandar, *Alvins s.n.* (SING). **Negeri Sembilan**: Senawang FR, *Yakim FMS 518* (K, KEP, SING); Sendayan FR, *FG Din 536* (BO, SING); Pasir Panjang, *Yusop FMS 4222* (KEP, SING); Gunung Angsi, *Zainuddin FRI 14591* (K, KEP, L, SING); Pasoh FR, *Nadiah et al. FRI 53951* (A, K, KEP, L, SAN, SAR, SING). ****Pahang**: Lesong FR, *Whitmore FRI 15851* (KEP); Rompin, *Ng FRI 22992* (KEP), *Ng FRI 22921* (KEP). **Perak**: loc. not. indicated, *Scortechini 1862* (SING); ibid., *Scortechini 1863* (SING); Selama, *Mat Said FMS 1250* (KEP); Chikus FR, *Speldenwinde 5366* (KEP); Changkat Jong FR, *Ng FRI 5644* (KEP); ibid., *Ng FRI 5878* (KEP, L); Bubu FR, *Selvaraj FRI 11154* (KEP, L); ibid., *Suppiah FRI 11675* (KEP); ibid., *Abdul Rahim KEP 86060* (KEP); Trong, *Everett FRI 13987* (K, KEP, L, SAN, SING); Teluk Intan, *Mohd Haniff SFN 14315* (SING); Bintang Hijau FR, *Kamarudin FRI 34556* (K, KEP, SAN, SAR). **Selangor**: Sungai Buloh FR, *Hamid FMS 1183* (KEP); ibid., *Strugnell FMS 7068* (KEP, SING); ibid., *Kiai FMS 8387* (KEP); ibid., *Foxworthy FMS 10213* (KEP); ibid., *Jamaat FMS 15311* (KEP); ibid., *DFO Klang FMS 18715* (KEP); ibid., *Strugnell 23931* (KEP); ibid., *Symington FMS 24445* (KEP); ibid., *Strugnell FMS 27880* (KEP); ibid., *Jamaat FMS 44944* (KEP); ibid., *Jamaat FMS 45002* (KEP); Bukit Cherakah FR, *Abu Amin FMS 18721* (KEP); Forest Research Institute Malaysia, *Ng FRI 33540* (KEP); ibid., *Motan KEP 94744* (K, KEP, L, SING). ****Terengganu**: Gunung Tebu FR, *Zainuddin FRI 17922* (K, KEP). SINGAPORE. Botanic Gardens, *Ridley 3887* (K, SING); ibid., *Mat s.n.* (SING); Bukit Mandai, *Corner s.n.* (SING), Bukit Timah, *Ridley 4738* (SING); Mandai Rd., *Kiah SFN 37112* (BO, KEP, SING). JAVA. Jakarta, cultivated in garden, *van Steenis 3105* (BO). – SUMATRA. **North Sumatra**: Atjeh, *Boschbouwproefstation bb. 8873* (BO). **South Sumatra**: Belinju, *Grashoff 48* (BO, L); Bajunglentjir, *Endert 276* (BO, L); ibid., *Grashoff 812* (BO, L); ibid., *Endert 85E. 1P. 754* (BO, BZF, K, L); ibid., *Boschbouwproefstation 1. PT. 788* (BO, L); Rawas, *Grashoff 1110* (BO, L). **East Sumatra**: Indrapura, *Volke 5* (BO, L); Jambi, *Roos TFB 2055* (L); Bandar Poelau, *Yates 2586* (K, L); Badjalinggi, *Lorzing 7397* (BO); Muarapantai, *Mol 23859* (BO, BZF, L); Indragiri, *Buwalda bb. 30081* (BO, BZF, L); Sungai Missingit, *Beguin 556* (BO, L). **West Sumatra**: Balaiselasa, *Boschbouwproefstation bb. 5969* (BO, L); Pariaman, *Boschbouwproefstation bb. 6736* (BO, L); Ophir, *Neth. Ind. For. Service bb. 19481* (BO, BZF, L, SING); ibid., *Djabar bb. 19629* (BO, BZF, L); Pengkalan Tapus, *de Haan bb. 29537* (BO, BZF, L); Malintang, *Korthals s.n.* (L); Between Bondjol-Lubuk Sikapang, *Teijsmann s.n.* (BO); Painan, *Boschbouwproefstation S.W.K./1–32* (BO, BZF, L); Air Manchur, *Beccari PS 620* (L); ibid., *Beccari PS 738* (BO, K, L) (type of *C. sumatrana* Becc.). – *BORNEO. **Sabah**: Kundasang, *Singh SAN 27495* (L, SAN); ibid., *Meijer SAN 37996* (SAN); ibid., *Fosberg SAN 44135* (L); Sosopodon, *Lajangah SAN 33145* (SAN); ibid., *Mikil SAN 38516* (K, L, SAN); ibid., *Mikil SAN 46782* (K, SAN); ibid., *Sinanggul SAN 47979* (SAN); Sunsuron, *Phillips SAN 89353* (SAN). **Sarawak**: Tg. Long Amok, *Rena George S 43060* (K, L, SAR); Lambir Hills NP, *Nadiah et al. S 100573* (KEP, SAR, SING). **Brunei**: River Ingei, *Wong WKM 607* (K, KEP, L, SAN); Labi Hills FR, *Coode et al. 6826* (K); Bukit Teraja, *Niga BRUN 15094* (SING); Pendayan FR, *Wyatt-Smith KEP 80130* (KEP); Bukit Biang, *Ashton BRUN 5584A* (BO, K, KEP, L, SAR, SING).

4. *Coelostegia kostermansii* Soegeng, Reinwardtia 5, 3 (1960) 277; Argent et al. (eds), Man. Non-Dipt. Trees Centr. Kalimantan 1 (1997) 97. TYPE: *Kostermans 12548*, Indonesia, East Kalimantan, West Kutei, Tudjung Plateau, Mt. Maranga (holo BO! iso A, CANB, K! KEP! L! NY, P).

Distribution. Endemic in Borneo (confined to Kalimantan).

Ecology. Primary forest on sandy loam soil, at 100–250 m.

Notes. C. kostermansii is morphologically very similar to *C. neesiocarpa* but consistently differs in having a rough-surface and distinctly 5-angled fruit (vs. smooth and rounded), elongate-ovoid seed with a caruncle up to 0.7 cm long (vs. ovoid with a caruncle up to 1.2 cm long), and slender slightly kneed petiole (vs. thick and strongly kneed petiole).

Specimens examined: BORNEO. **Kalimantan**: West Kalimantan, Mt. Maranga, *Kostermans 12548* (BO, K, KEP, L) (type); Mt. Damus, *Hallier 776* (BO). East

Kalimantan, Belajan River near Tabang, *Kostermans 10583* (L); Tabang, *Kostermans 10659* (L).

5. *Coelostegia montana* Sidiyasa, Blumea 46 (2001) 165. TYPE: *Sidiyasa & Arifin 1529,* Indonesia, East Kalimantan, Bulungan District, Kayan Mentarang National Park, Gunung Lunjut (holo WAN, iso BO!, K, L!).

Distribution. Endemic in Borneo (confined to Sabah, Sarawak and Kalimantan) (Fig. 1).

Ecology. In dipterocarp and submontane forests on well-drained ridges, on igneous (andesitic) derived soils, at 884–1450 m altitude.

Notes. Sidiyasa (2001) described *C. montana* based on fruiting specimens from Sarawak (*Anderson S 28461*) and fruiting specimens with young flower buds from Kalimantan (*Sidiyasa & Arifin 1529*). The recently collected specimens from Sabah (*Nadiah et al. SAN 149577*) bearing matured fruits and fully develop flowers represent a new record of this species for the state, thus extending its distribution in Borneo.

Coelostegia montana is closely related to *C. kostermansii* but can be distinguished by its c. 7–8 pairs of leaf lateral veins (vs. c. 9–13 pairs), narrowly obovate stipules, c. 6 mm long (vs. lanceolate stipules, c. 4 mm long), depressed conical and apically lobed flower buds c. 3 mm in diameter (vs. apiculate flower buds, up to 2 mm), and dark blue, subglobose fruits with rounded base (vs. yellowish green, ovoid fruits that are distinctly 5-angled at base).

Specimens examined: BORNEO. **Sabah**: Tambunan district, Rafflesia trail, *Nadiah et al. SAN 149577* (KEP, SAN). **Sarawak**: Kapit, Sungai Balleh, *Anderson S 28461* (BO, K, KEP, KLU, L, SAR). **Kalimantan**: East Kalimantan, Kayan Mentarang NP, Gunung Lunjut, *Sidiyasa & Arifin 1529* (BO, K, L, WAN) (type).

6. *Coelostegia neesiocarpa* Soegeng, Reinwardtia 5, 3 (1960) 279; Anderson, Checkl. Trees Sarawak (1980) 153; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 56; Argent et al. (eds), Man. Non-Dipt. Trees Centr. Kalimantan 1 (1997) 97. TYPE: *de Zwaan bb. 11288,* Indonesia, East Kalimantan, Bulungan, Rumah R. (holo BO! iso BZF!).

Distribution. Endemic in Borneo (confined to Sarawak and Kalimantan).

Ecology. In lowland forest at 100–300 m altitude, growing on dacite-derived alluvial fans in damp sandy valleys.

Notes. Coelostegia neesiocarpa differs from the other species in the genus in having an elliptic-ovate, coriaceous, concolorous leaves with rounded base; thick and strongly kneed petiole; subglobose fruits up to 14 cm long, 11 cm diameter, with a smooth surface and rounded base; and ovoid seeds with a caruncle c. 1.2 cm long.

Specimens examined: BORNEO. **Sarawak**: Hose Mountain, Mujong, Batu Kapal, *Ashton S 21242* (BO, K, L, SAR, SING). **Kalimantan**: East Kalimantan, Salimbata, Rumah R., *de Zwaan bb. 11288* (BO, BZF) (type); Upper Mahakam, *Henar bb. 20696* (BO, BZF).

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Appendix A. Morphological characters distinguishing the genera of the Durioneae-group in Borneo: *Coelostegia, Durio, Kostermansia* and *Neesia*. Sources: Kostermans 1958; Soegeng 1959, 1960; Soepadmo 1961; Baas 1972; Nilsson & Robyns 1986; Webster et al. 1996; Salma 1999, 2000; Sidiyasa 2001; Masliya 2008; Salmizawati 2008; Siti Fatimah 2008; Tan 2008.

Characters	*Coelostegia*	*Durio*	*Kostermansia*	*Neesia*
Buttresses	large, thin, convex, spreading	rounded, straight to concave, not spreading	up to 7 m high, plank-like, spreading	large, thin, convex, spreading
Leaf size (cm)	(4.5–)6–12(–14.8) × (1.1–)2–5(–6)	3–42.5 × 3–15	(6–)9–13(–19) × (2–)4–6(–9.5)	6–60 × 3–25
Lower leaf surface: pubescence	scales only	simple & stellate hairs, also scales	scales only	stellate hairs; rarely sparse minute long-fimbriate scales
Tertiary/ inter-costal veins	indistinct, reticulate	generally not prominent, reticulate	prominent, reticulate	distinct, reticulate
Midrib	evident, flat or raised above	sunken or channelled above	strongly prominent above	obscure, depressed above
Epicalyx	reduced in size, subtending calyx, 3-lobed at anthesis	completely enveloping flower bud, splitting into 2 lobes	partly enveloping flower bud, splitting into 2 lobes	completely enveloping flower bud, splitting into 2–5 lobes
Calyx-lobes/ sepals	induplicate-saccate	not induplicate-saccate	not induplicate-saccate	not induplicate-saccate
Corolla/ petals	shorter than calyx, calyptrate, perigynous	mostly showy, longer than calyx, free, long-persistent, hypogynous	shorter than calyx, not showy, free, caducous, hypogynous	shorter than calyx, hypogynous, calyptrate
Stamens (filament & anther)	longer than ovary; topped by three 1-celled anthers	longer than ovary; each filament with 1–many unilocular anthers	shorter than ovary; topped by two bean-shaped, basifixed, 2-celled anthers	longer than ovary; topped by one 2-celled anther
Ovary	partly embedded in receptacle, covered by peltate scales	superior, covered by peltate scales & stellate hairs	superior, covered by peltate scales	superior, covered by hirsute, stellate hairs
Style	conspicuous, filiform	well developed	reduced, or very short, thick	short, conical or filiform
Stigma	discoid, peltate, conspicuous	small, capitellate	large, convex, discoid, peltate	small, capitellate, round or subpentagonous

Fruit surface	spiny to muricate or smooth	covered with slender or stout spines	densely spiny	muricate or short-spiny
Fruit-valves inside	glabrous	glabrous	glabrous	with dense brownish, hirsute, prurient hairs
Fruit dehiscence	dehiscing to c. 1/2–1/3 of its length (valves split while fruit is still attached to tree, becoming erect or reflexed)	some fruits do not dehisce, or dehisce to the very base (generally dehiscent only after falling to the ground)	dehiscing to the base (valves split while fruit is still attached to tree, becoming erect or reflexed)	dehiscing to c. 1/2–1/3 of its length to ± completely (valves split while fruit is still attached to tree, becoming erect or reflexed)
Aril or caruncle	basal caruncle present	aril absent or present and covering half to whole seed	no aril / caruncle	basal caruncle present
Seeds	smooth, in 2 rows in each locule	ellipsoid, in 2 rows in each locule; large, pale brown to reddish black	few, large, glossy, dark brown (white when fresh)	ellipsoid, smooth
Cotyledons	thin, foliaceous, covered by 2 flat-convex lobes of the endosperm	thick, flat-convex, fleshy; endosperm absent	foliaceous, flat, covered by 2 partite endosperm	foliaceous, enveloped by 2 flat-convex lobes of the endosperm
Pollen type	*Durio*-type	*Durio*-type	*Kostermansia*-type	*Durio*-type
Type of apertures	3-colporate, short narrow colpus	3-colporate, short broad colpus	3-colporate, long narrow colpus	3-colporate, short narrow colpus
Pollen shape	prolate-spheroidal	oblate-spheroidal	oblate-spheroidal	prolate-spheroidal
Ornamentation of exine	microreticulate to smooth	smooth	microreticulate	microreticulate
Trichomes (on lower leaf surface)	dentate-peltate scales & glandular hairs	stellate & dentate peltate scales; appressed stellate & simple hairs; glandular hairs	subentire peltate scales & glandular hairs	appressed stellate, dendritic, simple & glandular hairs
Stomata type	anisocytic, tetracytic	paracytic	amfiparacytic	anisocytic, tetracytic
Stomata on lower leaf surface	randomly arranged	randomly arranged	in circles around trichome bases	randomly arranged

A synopsis of *Jarandersonia* (Malvaceae: Brownlowioideae)

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ABSTRACT. A revision of *Jarandersonia* was conducted as part of a study of Malvaceae: Brownlowioideae for the Tree Flora of Sabah and Sarawak Project. Six species of *Jarandersonia* are recognised for Borneo, of which *J. pentaceoides* R.C.K.Chung & H.S.Tan, endemic to central Kalimantan, is new to science. A complete list of exsiccatae, nomenclatural and taxonomic notes, geographical distribution and conservation status of the recognised species, are provided.

Keywords. Borneo, Brownlowioideae, *Jarandersonia*, Kalimantan, Malvaceae, tree flora

Introduction

Jarandersonia was first described by Kostermans in 1960 based on the Sarawak species, *J. paludosa* (now a synonym of *J. purseglovei* (Kosterm.) Kosterm.). In the past fifty years, the genus had been included in the family Tiliaceae. Recently, molecular evidence has supported the inclusion of *Jarandersonia* in the subfamily Brownlowioideae of the expanded family Malvaceae *s.l.* based on *ndhF*, *atp*B and *rbc*L data (Alverson et al. 1999; Bayer et al. 1999; Nyffeler and Baum 2000; Bayer and Kubitzki 2003). In Malaysia, Brownlowioideae consists of five genera, namely *Berrya*, *Brownlowia*, *Diplodiscus*, *Jarandersonia* and *Pentace*, and has about 55 species. The genus *Jarandersonia* can be easily distinguished from *Brownlowia*, *Diplodiscus* and *Pentace* by its elliptic or obovate leaves, densely hairy fruit spines and a combination of micromorphological characters.

Jarandersonia, locally known as *baru baran* (Iban) in Sarawak, was named after J.A.R. Anderson, a forest botanist working in Sarawak and Brunei from 1951 to 1970. Kostermans (1962, 1970) described three more species and transferred *Brownlowia clemensiae* Burret to the genus, making a total of five known species of *Jarandersonia*. In our recent revision of the genus for the Tree Flora of Sabah and Sarawak Project, an additional new species, *J. pentaceoides* R.C.K.Chung & H.S.Tan, from central Kalimantan was discovered. In an assessment of the conservation status of the five species, one was found to be critically endangered, two endangered, one vulnerable, and one of least concern.

Synopsis of species

Jarandersonia Kosterm., Reinwardtia 5 (1960) 319, Reinwardtia 8 (1970) 17; Hutchinson, Gen. Flow. Pl. 2 (1967) 491; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 448; Bayer & Kubitzki *in* Kubitzki (ed.), Fam. Gen. Vasc. Pl. 5 (2003) 258; LaFrankie, Trees of Tropical Asia (2010) 479. TYPE SPECIES: *Jarandersonia paludosa* Kosterm. [= *Jarandersonia purseglovei* (Kosterm.) Kosterm.].

Vernacular name. Baru baran (Iban, Sarawak).

Distribution. The genus comprises six species endemic to Borneo (2 are in western Sarawak, 1 Sabah, 1 Sarawak and Kalimantan, 1 Sarawak, Brunei and west Kalimantan, 1 central Kalimantan). (Fig. 1)

Ecology. Mainly found in mixed dipterocarp forest and peat swamp forest.

Notes. The terminology used for trichome types mainly follows Webster et al. (1996). Three main trichome types were observed in *Jarandersonia*, namely, subentire-lepidote (radii webbed 80–100%), dentate-lepidote (radii webbed 50–80%) and stellate-lepidote (radii webbed 30–50%).

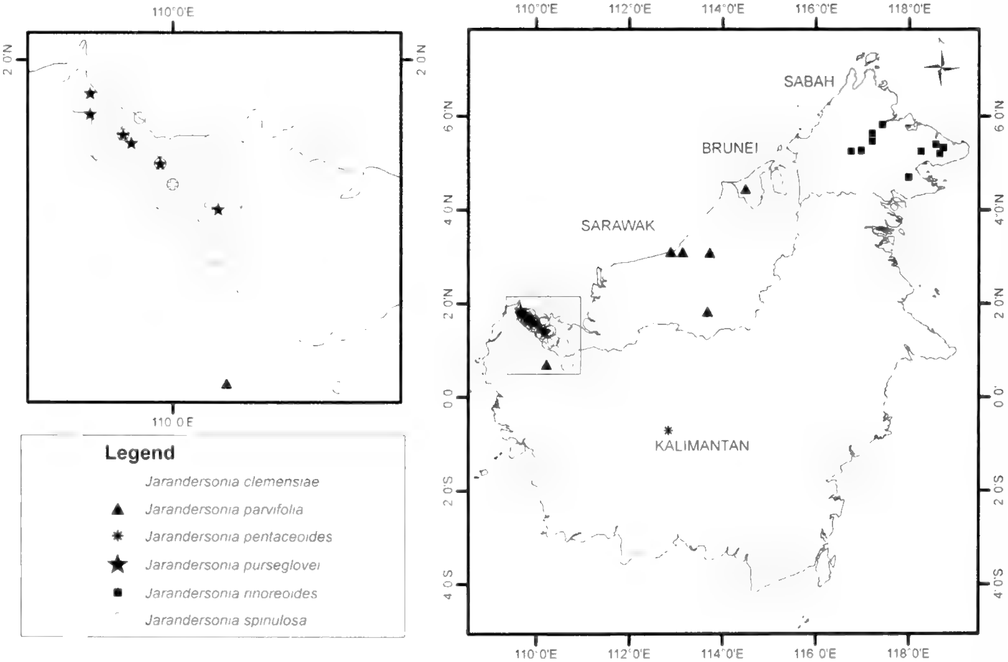

Fig. 1. Known distribution of *Jarandersonia* species in Borneo (right). Species distributions in the south-western part of Sarawak are shown in magnified view (left).

1. ***Jarandersonia clemensiae*** (Burret) Kosterm., Reinwardtia 8 (1970) 18; Anderson, Checkl. Trees Sarawak (1980) 339; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 448; Whitmore et al., Tr. Fl. Indonesia Checkl. Kalimantan 2, 1 (1990) 356; Rantai & Chai, New Checkl. Trees Sarawak (2007) 333. *Brownlowia clemensiae* Burret, Notizbl. Bot. Gart. Berl.-Dahl. 13 (1936) 252; Kostermans, Communic. For. Res. Inst. Bogor 73 (1961) 29, fig. 23; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 432. TYPE: *J. Clemens & M.S. Clemens 22202*, Borneo, Sarawak, Mt Gading (holo B†; iso BO, K, NY barcode 00415382, SAR). (Fig. 2A)

Vernacular names. *Baru baran* (Iban), *nginjoaja* (Bidayuh Padawan, Sarawak).

Distribution. Endemic to Borneo (Sarawak and Kalimantan). In Sarawak, known from Lundu, Kuching, Bau, and Serian districts. Also occurring in Kalimantan.

Conservation status. Least concern. Most of the populations are found in protected areas.

Ecology. In lowland mixed dipterocarp forest, in riparian and secondary forests. Very local, usually along small stream banks on clay-rich alluvium, to 200 m altitude.

Notes. Jarandersonia clemensiae is closely related to *J. purseglovei*. The former, however, differs from the latter in having a subcordate leaf base (vs. acute to rounded), 12–16 pairs of lateral veins (vs. 18–23 pairs), flattened lateral veins above (vs. sunken above), rounded midrib (vs. square) and unbranched fruit spines with stellate-lepidote and dentate-lepidote trichomes (vs. short-branched with branch tips bearing simple or 2-armed setose hairs).

2. ***Jarandersonia parvifolia*** Kosterm., Reinwardtia 8 (1970) 18; Anderson, Checkl. Trees Sarawak (1980) 339; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 448; Whitmore et al., Tr. Fl. Indonesia Checkl. Kalimantan 2, 1 (1990) 356; Rantai & Chai, New Checkl. Trees Sarawak (2007) 333. TYPE: *Ilias S 15561*, Borneo, Sarawak, Bintulu, Segan FR (holo BO; iso A, SAN, SAR, SING). (Fig. 2B)

Vernacular name. Baru baran mit (Iban, Sarawak).

Distribution. Endemic to Borneo (Sarawak, Brunei and Kalimantan). In Sarawak, known from Bintulu, Tatau and Kapit districts. Also occurring in Brunei and Kalimantan.

Conservation status. Critically endangered A2c. Two localities had been converted to oil palm plantations. Details for the remaining localities are scanty.

Ecology. In mixed dipterocarp forest, on leached yellow clay soils, to 700 m altitude.

Notes. Jarandersonia parvifolia can be easily distinguished by its small elliptic to broadly elliptic leaves, 4–11.5 × (1.4–)2–5 cm and square midrib in cross-section.

3. *Jarandersonia pentaceoides* R.C.K.Chung & H.S.Tan, Syst. Bot. (in press). Proposed Type: *J.K. Jarvie & A. Ruskandi 5769*, Borneo, Kalimantan, Kalimantan Tengah, Samba (holo KEP; iso A, BO, K, SAN, SING). (Fig. 2C)

Distribution. Known only from the type, recorded in Samba, central Kalimantan.

Ecology. Primary forest, hilly terrain on red clay soil with slope, at attitudes to 300 m.

Notes. Jarandersonia pentaceoides is most similar to *J. rinoreoides*, having cuneate leaf base, rounded midrib, slender and unbranched fruit spines. However, *J. pentaceoides* is distinct in having densely stellate-lepidote and dentate-lepidote trichomes along the edges of tertiary veins and honeycomb-like quaternary veins on the lower leaf surface, a kneed petiole that is swollen at both ends, and a sparsely stellate-lepidote and tufted hairy seed coat, whereas in *J. rinoreoides* the quaternary veins are absent, the petiole is straight and not swollen at both ends and the seed coat is glabrous. The leaves of *J. pentaceoides* are similar to those of some common *Pentace* and *Mallotus* (i.e., *M. leucodermis* Hook.*f.* and *M. muticus* (Müll.Arg.) Airy Shaw) in shape, number of secondary veins, and its kneed petiole that is swollen at both ends. However, the morphological characters of *J. pentaceoides* do not match the features of both *Pentace* and *Mallotus*, because the new species have distinct quaternary veins (vs. absent in both *Pentace* and *Mallotus*) and spiny fruits (vs. winged fruits in *Pentace* and shortly stiff spiny in *Mallotus*). The fruit spines of *J. pentaceoides* are similar to *Commersonia bartramia* (L.) Merr. but the former can be easily distinguished by its cuneate leaf base (vs. cordate) and indehiscent fruit (vs. splitting open fruit into 5 valves).

4. *Jarandersonia purseglovei* (Kosterm.) Kosterm., Reinwardtia 6 (1962) 299; Anderson, Checkl. Trees Sarawak (1980) 339; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 449; Whitmore et al., Tr. Fl. Indonesia Checkl. Kalimantan 2, 1 (1990) 356; Rantai & Chai, New Checkl. Trees Sarawak (2007) 333. *Brownlowia purseglovei* Kosterm., Gard. Bull. Singapore 17 (1958) 1, Communic. For. Res. Inst. Bogor 73 (1961) 28, fig. 22. TYPE: *J.N. Purseglove P 4662*, Borneo, Sarawak, Mt Pueh (holo SING barcode 0050678; iso BO). (Fig. 2D)

Jarandersonia paludosa Kosterm., Reinwardtia 5 (1960) 319. TYPE: *J.A.R. Anderson S 6554*, Borneo, Sarawak, Lundu district (holo K; iso BO, L, SAR, SING barcode 0050679).

Vernacular names. Baru baran kasar, baru barun daun kasar (Iban, Sarawak).

Distribution. Endemic to Borneo (W Sarawak). Recorded from Lundu, Kuching and Bau districts.

Conservation status. Endangered A2c, due to loss of natural habitat and its population size having been reduced by more than 50%.

Ecology. Lowland mixed dipterocarp forest, on shallow peat and ground-water podsols near sea-level.

Notes. The leaves of *Jarandersonia purseglovei* are very similar to those of *Durio oblongus* Mast. (Malvaceae: Helicterioideae Durioneae). However, the species can be distinguished from *D. oblongus* by the cuneate leaf base (vs. rounded), rounded midrib (vs. ridged) and prominent intermediate veins (vs. inconspicuous). This species is also closely related to *J. clemensiae* (see note under *J. clemensiae*).

5. *Jarandersonia rinoreoides* Kosterm., Reinwardtia 8 (1970) 17; Whitmore et al., Tr. Fl. Indonesia Checkl. Kalimantan 2, 1 (1990) 356. TYPE: *W. Meijer SAN 27885*, Borneo, Sabah, Sandakan, Tabin, W of Sulap (holo SAR; iso K, KEP barcode 76031, L, SAN). (Fig. 2E)

Distribution. Endemic to Borneo (Sabah). Recorded from Labuk Sugut, Sandakan, Kinabatangan and Lahad Datu districts.

Conservation status. Vulnerable B1ab(iii). The species is found in less than 10 locations that are not strictly protected.

Ecology. In mixed dipterocarp forest, usually near streams, to 700 m altitude.

Notes. Jarandersonia rinoreoides is closely related to *J. spinulosa* but differs in its midrib and lateral veins (glabrous vs. pilose hairy above), and its fruit spines (slender, tufted hairy intermixed with simple or 2(–3)-armed setose hairs, unbranched vs. stout, glabrous, branched with branch tips bearing simple or 2-armed setose hairs).

6. *Jarandersonia spinulosa* Kosterm., Reinwardtia 6 (1962) 300; Anderson, Checkl. Trees Sarawak (1980) 339; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 449; Whitmore et al., Tr. Fl. Indonesia Checkl. Kalimantan 2, 1 (1990) 357; Rantai & Chai, New Checkl. Trees Sarawak (2007) 333. TYPE: *H.N. Ridley s.n.*, Borneo, Sarawak, Mt Matang (holo K). (Fig. 2F)

Distribution. Endemic to Borneo (Sarawak). In Sarawak, known from Kuching and Bau districts.

Conservation status. Endangered B2ab(iii). The species is known from only two specimens with the latest collection made in 1985. No populations are known to occur in the network of protected areas and some of the forest reserves where this species occurs are small and fragmented. No ecological details were available.

Ecology. Lowland mixed dipterocarp forest, along rivers, to 50 m altitude.

Note. This species is closely related to *J. rinoreoides* (See note under *J. rinoreoides*).

Identification list

Numbers after the collector numbers refer to the following *Jarandersonia* species: 1 = *J. clemensiae*; 2 = *J. parvifolia*; 3 = *J. pentaceoides*; 4 = *J. purseglovei*; 5 = *J. rinoreoides*; 6 = *J. spinulosa*. When collection numbers are not available, dates are given within brackets.

Aban SAN 97250: 5; *Anderson S 25415*: 1; *S 26759*: 1; *S 6554*: 4; *Awang Enjah S 68042*: 1. *Buxton A 548*: 1; *Bojeng S 9355*: 1. *Clemens & Clemens 22202*: 1. *Dewol SAN 99462*: 5. *Frodin & Othman 2027*: 1; *Fordin et al. 2119*: 1; *Fuchs 21376*: 2. *Guijing SAN 45510*: 5; *SAN 45511*: 5; *SAN 45518*: 5. *Ilias S 15561*: 2. *Jacobs 5567*: 1; *Jaamat & Tachun FMS 39640*: 2; *James S 29846*: 1; *Jarvie & Ruskandi 5769*: 3; *Jong 904*: 1; *Jugah S 51590*: 1. *Lakising SAN 70168*: 5. *Meijer SAN 27885*: 5; *SAN 31016*: 5; *SAN 51237*: 5; *SAN 53222*: 5; *Madani SAN 61097*: 5; *Munting S 54250*: 1. *Othman S 37050*: 1; *S 37820*: 4; *S 40042*: 1; *Othman et al. S 49899*: 1; *S 63818*: 1; *Othman & Munting S 54348*: 2; *S 54349*: 2. *Purseglove P 4662*: 4. *Rantai et al. S 68437*: 1; *Reto et al. 506*: 1; *508*: 1; *511*: 4; *Ridley s.n.* (1/1915): 6. *Sigin & Lidah SAN 97197*: 5; *Sinanggul SAN 57101*: 5; *Suah SAN 37379*: 5. *Tukirin & Partomihardjo K 3319*: 2. *Yahud et al. S 93215*: 1; *S 93216*: 1; *S 93218*: 1; *S 93223*: 4; *S 93224*: 1; *S 93226*: 1; *S 93227*: 1; *S 93228*: 4; *S 93229*: 4; *S 93231*: 1; *S 93263*: 1; *Yassin s.n.*(5/1969): 2; *Yii S 51263*: 6.

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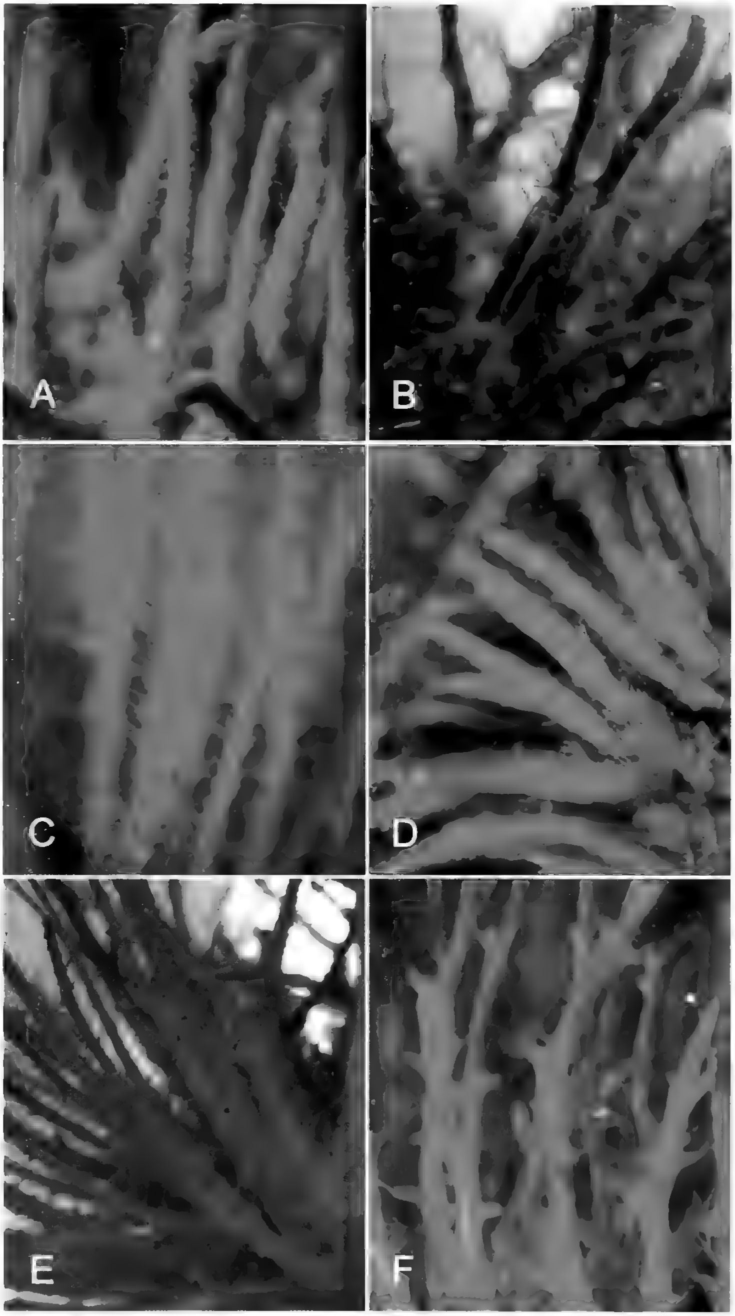

Fig. 2. Fruit spines of *Jarandersonia* species. **A.** *J. clemensiae*, spines stout, stellate-lepidote and dentate-lepidote, unbranched. **B.** *J. parvifolia*, spines stout, tufted hairy, short-branched with the branch tips bearing simple or 2(–3)-armed setose hairs. **C.** *J. pentaceoides*, spines slender, stellate-lepidote with simple setose hairs, unbranched. **D.** *J. purseglovei*, spines stout, tufted hairy, short-branched with the branch tips bearing simple or 2-armed setose hairs. **E.** *J. rinoreoides*, spines slender, tufted hairy intermixed with simple or 2(–3)-armed setose hairs, unbranched. **F.** *J. spinulosa*, spines stout, glabrous, short-branched with the branch tips bearing simple or 2-armed setose hairs.

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Towards an account of Sapotaceae for Flora Malesiana

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ABSTRACT. An overview of the pan-tropical family Sapotaceae is provided with particular focus on the Malesian region. Past and current taxonomic and phylogenetic research is summarised and publications relating to the production of a Flora Malesiana Sapotaceae account highlighted. Challenges to delivering a Flora Malesiana account are identified and some potential solutions suggested.

Keywords. Flora Malesiana, Sapotaceae, systematics, taxonomy

Introduction

Sapotaceae is a pantropical family of trees and shrubs and is composed of about 50 genera and 1000 species. In Malesia there are an estimated 15 genera and 300 species. The family is ecologically important with representatives of the family common in the forests of Malesia. They occur from beach forests at sea level to mossy montane forests at over 4000 m altitude. The family is economically important and produces the important heavy hardwood timber, *Bitis* (mainly *Madhuca utilis* (Ridl.) H.J.Lam, *Palaquium ridleyi* King & Gamble and *Palaquium stellatum* King & Gamble) and the light to medium hardwood, *Nyatoh*, from many other species (Ng 1972). The family also produces edible fruit with *Manilkara zapota* (L.) P.Royen (sapodilla plum, *ciku*), and *Chrysophyllum cainito* L. (star apple), introduced from Central America, the most widely cultivated. The latex produced from *Palaquium gutta* (Hook.) Burck (Gutta Percha) has been used in the insulation of cables, golf balls and in root fillings in dentistry (Burkill 1966, Boer & Ella 2000).

It is a family which has historically been acknowledged as being taxonomically problematic (Pierre 1890; Baillon 1891; Dubard 1912, 1915; Lam 1939; Aubrévile 1964; Baehni 1965; Pennington 1991). Although species tend to be relatively well defined, the genera are not. Estimates of number of genera range from 122 (Aubrévile 1964) to 53 (Pennington 1991). There is a high level of homoplasy in the family and unique synapomorphies for genera are rare with most being distinguished on character-state combinations.

The family can be quite readily identified in the field by the white exudate (latex) produced from the cut bark and twigs, the spirally arranged leaves which are usually crowded at the tips of twigs and the often coppery underside of leaves. The flowers are in axillary fascicles usually behind the leaves and in fruit the calyx and style are persistent. The calyx provides a good taxonomic character at generic and tribal levels and seed shape and the position and extent of the seed scar provide useful characters at the generic and species level (Pennington 1991).

Monographic studies

Most monographic work on the family in Malesia was undertaken by researchers based at the Rijksherbarium, Leiden from the 1930's to early 1960's. Over this period many papers were published in Blumea as part of the series "*Revision of the Sapotaceae of The Malaysian Area in a Wider Sense*". In these publications, the geographical area covered was much larger than what we today term Malesia and included areas such as the Solomon Islands, New Caledonia and Fiji.

The most important contributors include the director of the Rijksherbarium between 1933 and 1962, Herman Johannes Lam. He published important revisions of genera in the Sapotaceae including *Manilkara* (Lam 1941a) and *Burckella* (Lam & Royen 1952a). He also produced family accounts for *Sapotaceae of the Dutch East Indies* (Lam 1925, 1927), *New Guinea* (Lam 1932) *and the Pacific Islands* (Lam 1942), a paper on the *Phylogenetics of Sapotaceae* (Lam 1935) as well as several notes on a range of other genera (Lam 1938, 1939, 1943a, 1943b, 1957). He also published taxonomic accounts of the closely related family Sarcospermataceae including a *Revision of Sarcospermaceae* (Lam & Varossieau 1938, 1939; Lam 1941b) and an account of Sarcospemataceae for Flora Malesiana (Lam 1948).

A co-worker of Lam's, Pieter van Royen, revised many large genera of Sapotaceae including *Planchonella* (Royen 1957a), *Palaquium* (Royen 1960a) and *Madhuca* (Royen 1960b). He also revised several other smaller genera such as *Burckella* (Lam & Royen 1952a, 1957b; Royen 1959), *Mimusops* (Royen 1952), *Manilkara* (Royen 1953, 1957c), *Xantolis* (Royen 1957d), *Diploknema* (Royen 1958a), *Aulandra* (Royen 1958b), *Eberhardtia* (Royen 1960d) and *Mastichodendron* (Royen 1960c) and compiled an account of Sapotaceae covering some 16 genera and 260 species for Flora Malesiana which was never published (Royen, Unpub.).

Willem "Wim" Vink started to revise van Royen's unpublished account but due to the large number of new forestry collections coming from the Malesian region, the many new species needing to be described and the many poorly known species needing new description, this could not be brought to fruition within the year allocated to the task. Several revisions of smaller genera such as *Leptostylis*, *Pycnandra* and *Magodendron* (Vink 1957) and *Chrysophyllum* (Vink 1958), however, were published and important contributions continue to be made by him (Vink 1995, 2001, 2002). Other Rijksherbarium researchers who published important works on Sapotaceae include van den Assem who revised *Ganua* (Assem 1953, Assem & Kostermans 1954), Jeuken who revised *Isonandra* (Jeuken 1952); Bruggen (1958a, 1958b) who revised *Payena* and *Aesandra*, and Herrmann-Erlee who revised *Krausella* and *Pouteria* (Herrmann-Erlee & Lam 1957, Herrmann-Erlee & Royen 1957).

One of the most important publications covering Sapotaceae throughout its distribution is *The Genera of Sapotaceae* (Pennington 1991). Based on morphology, this reviewed the whole family and brought much clarity to the genera. It recognised 53 genera and 5 tribes and considered *Sarcosperma* to be part of Sapotaceae (not Sarcospermataceae). In Malesia, all 5 tribes are represented with Isonandreae containing most Malesian genera. Based on this work, the *World Checklist of Sapotaceae* was produced (Govaerts et al. 2001), as well as the related website (http://apps.kew.org/wcsp/home.do).

Molecular phylogenetic studies

The first large-scale molecular studies of Sapotaceae were produced by Anderberg & Swenson (2003) and Swenson & Ardenberg (2005). Based on molecular and morphological data, they proposed a new subfamily classification of Sapotaceae with three subfamilies being recognised, Sarcospermatoideae, Sapotoideae and Chrysophylloideae. Malesian genera are found in all three subfamilies. The sampling from Malesia, however, was poor with only 5 taxa represented. The two largest genera in Malesia, *Madhuca* and *Palaquium* had only a single species sampled and these were from outside the Malesian region. Swenson and co-workers have published several other important phylogenetic studies on the subfamily Chrysophylloideae especially from New Caledonia (Bartish & Swenson 2005, Swenson & Bartish 2007, Swenson & Munzinger 2007). Also researching the subfamily Chrysophylloideae, Triono et al. (2007) produced a molecular phylogeny of *Pouteria* from Malesia and Australasia to re-assesses the generic delimitation of *Pouteria* and its affinities with *Planchonella*. This did not support the broad circumscription of *Pouteria* by Pennington (1991).

Smedmark & Anderberg (2006, 2007) published work on the subfamily Sapotoideae and provided a useful backbone to research on the subfamily but again few samples were included from the Malesian region. This is being addressed by the author and co-workers at the Royal Botanic Garden Edinburgh (RBGE) who have substantially increased sampling of genera from the Malesian region, in particular from Pennington's tribe Isonandreae (Wilkie et al., in prep.). This will be used to help establish a robust generic and infrageneric framework to facilitate future monographic research on the family in Malesia. Researchers at RBGE are also using this data to investigate biogeographic patterns within Isonandreae (Richardson et al., in prep.).

Floristic studies

Several floristic accounts of the family have been produced in the Malesian region. *The Tree Flora of Malaya* (Ng 1972) covered 11 genera and 76 species and kept *Sarcosperma* in the Sarcospermaceae, the *Manual of the Larger and More Important non Dipterocarp Trees of Central Kalimantan* (Argent et al. 1997) covered 5 genera and 36 species, and the *Tree Flora of Sabah and Sarawak* (Chai & Yii 2002) covered 11 genera and 120 species, including *Sarcosperma*. Two further flora accounts are in preparation. The Sapotaceae account for the *Flora of Peninsular Malaysia* will cover an estimated 11 genera and more than 80 species and will have contributions from a wide range of Malaysian taxonomists (Wilkie et al., in prep.) and the *Flora of Thailand* Sapotaceae account covering 9 genera and 45 species (Chantaranothai 1999) is due to be published by 2011 (Chantaranothai, in prep.).

Challenges to delivering a Flora Malesiana account

An account of Sapotaceae for Flora Malesiana with an estimated 15 genera and 300 species is clearly deliverable; however, there are several issues that need to be addressed if a modern account is to be produced. The first is the development of a robust generic framework within Sapotaceae. It has been recognised that generic limits are problematic and that the circumscription of several genera are still not clarified fully. Recent molecular phylogenetic studies are helping address this but much still needs to be done, in particular increased sampling of taxa found in the Malesian region. A second challenge is that previous sectional classifications of genera by authors such as Dubard (1909), Lam (1925), van Royen (1960a) are not congruent with recent molecular phylogenies (Wilkie et al., in prep). This makes producing taxonomic accounts of large genera such as *Madhuca* and *Palaquium* difficult. It is therefore important that new sectional classifications are developed for these genera so that taxonomists can work with groups of manageable size. Finally, there is still a lack of good fertile material for many Malesian taxa. If full taxonomic descriptions are desired, a detailed collecting programme for the family is needed, in particular from the under-collected areas of East Malesia.

Facilitating the production of a Flora Malesiana account

For taxonomists to contribute to the Flora Malesiana Sapotaceae account, they need access to specimen information, access to the actual specimens and access to the literature. Over the past two years, RBGE has been trying to address these issues largely through the establishment of the Sapotaceae Resource Centre (www.sapotaceae.info). This brings together Sapotaceae specimen data held by various institutes in Malesia and Europe (E, K, KEP, L, SAN, SAR, SING) as well as from individuals who have worked on Sapotaceae. To date, access to over 45,000 Sapotaceae specimen records is available via the website. The data is constantly being updated and cleaned as it is used for projects such as the Flora of Peninsular Malaysia.

A large collection of Sapotaceae herbarium specimen images has also been gathered. In order that they are as accessible to as many people as possible, these are being linked to specimen information on the website. However, with over 16,000 Sapotaceae herbarium specimen images from Malesia, this will take some time. The most effective and efficient way to make these images available on the web is constantly being reviewed.

A library of some 500 Sapotaceae reprints built up over 30 years by T.D. Pennington and V. Wink has been converted to PDF format and the best way to share this information (taking into account copyright issues and other international projects such as the Biodiversity Heritage Library) is currently being investigated.

The delivery of a Flora Malesiana Sapotaceae account will require the enthusiasm and commitment of taxonomists from the Malesian region, particularly those at an early stage in their career. The Sapotaceae Resource Centre is designed to stimulate interest in the family as well as link Sapotaceae researchers together.

Conservation assessments

Taxonomists should not just be in the business of documenting plants before they are gone—they need to be doing more to make sure they don't go in the first place. Integral to the Flora Malesiana Sapotaceae account has to be the production of Conservation Assessments (IUCN 2001) as these can lead to long-term monitoring of species and their active conservation (e.g., Chan 2007; Chua et al. 2009, 2010).

Conclusion

Delivering an account of Sapotaceae is achievable in the medium term. However, this will require the commitment of a substantial amount of time by researchers. To help this happen, the objectives of Flora Malesiana need to be embedded and championed by many more institutes. Taxonomists from Malesia also need to be much more involved in producing accounts than has traditionally been the case. This will require financial support. Flora Malesiana as the *collective voice* of Malesian taxonomy is ideally placed to address these concerns and to help leverage funding from global initiatives to achieve these aims.

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Precursor to flora account of *Procris* (Urticaceae) in Peninsular Malaysia

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ABSTRACT. A review of *Elatostema* J.R.Forst. & G.Forst. and *Procris* Juss. (Urticaceae) occurring in Peninsular Malaysia resulted in four taxa, currently classified in *Elatostema*, being transferred to the genus *Procris*. Six species of *Procris* are recognised as occurring in Peninsular Malaysia with the following new combinations provided here: *Procris acaulis* (Hook.f.) B.J.Conn & J.T.Hadiah; *Procris curtisii* (Ridl.) B.J.Conn & J.T.Hadiah; and *Procris repens* (Lour.) B.J.Conn & J.T.Hadiah. A modified description of *Procris* (including *Pellionia*) and a key to the species occurring in Peninsular Malaysia are provided.

Keywords. *Elatostema*, *Pellionia*, Peninsular Malaysia, *Procris*, Urticaceae

Introduction

Elatostema is a very large genus that is considered to consist of approximately 300 herbaceous and sub-shrubby species (Friis 1993) that are characterised by having female flowers arranged on a flattened discoid or lobed receptacle. It is the type genus of the Tribe Elatostemateae (Conn & Hadiah 2009). *Elatostema* is widely distributed throughout the tropical, subtropical and sub-temperate regions from the west to east coast of Africa, Madagascar and Mascarene Islands, through Sri Lanka, southern India, tropical Himalaya, Bangladesh, Myanmar to South-East Asia, Micronesia, then throughout Papuasia, to eastern Australia, New Caledonia, northern New Zealand, and Polynesia. It also occurs in subtropical and sub-temperate regions of China, Taiwan and Japan. Since it was first described by Forster & Forster (1775), the taxonomic circumscription of the genus and infrageneric taxa have been problematic. The generic description includes features of what is now regarded as the separate genus *Procris*. In the protologue of *Elatostema*, the species *Elatostema pedunculatum* and *E. sessile* were described. *Elatostema pedunculatum* was circumscribed as having flowers with 5 stamens ('*pentandrum*'), whereas the flowers of *E. sessile* have 4 stamens ('*tetrandrum*'). The former species was later transferred to the genus *Procris* (Weddell 1856), whereas the latter remained in *Elatostema*. Furthermore, the taxonomic distinction of the related taxa, *Elatostematoides*, *Pellionia* and *Procris* has continued to be problematic.

The first, and most complete account of the taxonomy of *Elatostema* was provided by Schröter & Winkler (1935, 1936). They modified the subgeneric division of previous workers (Hallier 1896, Winkler 1922) and proposed four subgenera, namely, subg. *Elatostema* (as '*Euelatostema*'), subg. *Elatostematoides,* subg. *Pellionia,* and subg. *Weddellia.* This division was primarily based on the nature of the leaves, stipules, inflorescence and the presence and form of the receptacle. Some authors maintain *Pellionia* as a distinct genus, for example, Wang (1980); Yahara (1984); Chen et al. (2003). The latter authors circumscribed *Pellionia* as having cymose female inflorescences, rarely with discoid receptacle and involucres, whereas the female inflorescences of *Procris* are capitate or globose and lack an involucre. Furthermore, the female flowers of *Pellionia* have (4 or) 5 perianth lobes, whereas female flowers of *Procris* have 3 or 4 perianth lobes. Schröter & Winkler (1935, 1936) recognised *Procris* as a separate genus. Based on chloroplast sequence data, preliminary analyses of relationships within *Elatostema* do not support the recognition of the subgenus *Pellionia* (Hadiah et al. 2003). Hadiah et al. (2008) concluded that there are four genera within the Tribe Elatostemateae, namely *Elatostema*, *Lecanthus*, *Pilea* and *Procris*, with *Pellionia* reduced to the synonymy of the last mentioned genus.

Materials and methods

Herbarium collections held at BO, K, KEP, NSW, SING were examined. Descriptive data are managed by DeltaAccess 2.0 software (Hagedorn 2007 onwards).

An identification key to the genera of the tribe *Elatostemateae* occurring in Peninsular Malaysia is provided. A brief description of *Procris* and a key to species recognised for Peninsular Malaysia, together with a list of selected specimens examined, are provided.

Distinguishing features of *Elatostema* and *Procris*

The following key summarises the diagnostic features of the genera of tribe *Elatostemateae* that occur in Peninsular Malaysia, namely, *Elatostema*, *Pilea* and *Procris* (including *Pellonia*).

Key to genera of tribe Elatostemateae

1a. Leaves opposite, more or less isophyllous; lamina ± equal basally; venation 3-pli-nerved .... *Pilea*

1b. Leaves appearing alternate, anisophyllous, with nanophyll reduced, and usually soon caduous; lamina very unequal basally; venation pinnate 2

2a. Perianth lobes of female flowers usually 4 or 5, much shorter than ovary, or strongly reduced, not corniculate at apex; achene 6–10-ribbed; male inflorescences usually with receptacle, rarely cymose; receptacle of female inflorescences discoid .... *Elatostema*

2b. Perianth lobes of female flowers 3–5, longer than ovary, usually corniculate below apex; achene tuberculate or striate, rarely smooth, never ribbed; male inflorescences cymose; receptacle of female inflorescences globose or head-like .. .. *Procris*

Species of *Procris* in Peninsular Malaysia

In the account of the Urticaceae for the Malay Peninsula by Ridley (1924), four species of *Pellionia*, five species of *Elatostema* and two species of *Procris* were recognised. Turner (1995) provided an updated catalogue of species of Urticaceae that were reported to occur in this region. In his catalogue, he listed 11 species of *Elatostema* (including taxa previously recognised as belonging to *Pellionia*) and two species of *Procris*. In this review of Turner's list of species for these two genera, four species listed as *Elatostema* are here transferred to *Procris*, resulting in six species being recognised for this region.

Procris Commers. ex Juss., *Genera Plantarum* 403 (1789); Schröter, *Repertorium Specierum Novarum Regni Vegetabilis* 45: 179–192 and 257–300 (1938), partly revised.
TYPE SPECIES: *Procris axillaris* J.F.Gmel., *Systema Naturae* 2: 267 (1791).

Shrubs, self-supporting (erect/suberect), terrestrial or epiphytic, monoecious or dioecious; branched and stinging hairs absent; internodes elongate, distinct. Stipules caducous, free, axillary, intrapetiolar. Leaves subopposite to alternate, petiolate; lamina not lobed; base oblique; margin toothed or entire; apex variable, leaf surface glabrous or hairy; venation symmetric, secondary vein pinnate. Nanophylls present, often not persistent. Cystoliths linear. Flowers unisexual. Male inflorescences distinctly pedunculate, paniculate (usually openly branched), branching unordered; involucral bracts absent. Male flowers actinomorphic; tepals 4 or 5, free; stamens 4 or 5, inflexed; rudimentary ovary present. Female inflorescences pedunculate or sessile, head-like (condensed); involucral bracts absent. Female flowers actinomorphic (or slightly asymmetrical); tepals 3–5, equal, connate (at least in part); staminodes present; ovary straight; style absent; stigma oblong, filiform to linear. Achene enclosed by perianth (or almost so) or not enclosed by perianth, smooth or variously rough.

Distribution. Central western and eastern Africa, Madagascar to Sri Lanka and India, Myanmar, southern China, Taiwan, throughout South-East Asia, Papua New Guinea, Solomon Islands, New Caledonia, and east throughout south-west Pacific islands.

Key to species of *Procris* in Peninsular Malaysia

1a. Leaf petiolate 2
1b. Leaf sessile or subsessile 5

2a. Nanophyll appearing absent, not persistent, soon dehiscent 3
2b. Nanophyll present and persistent .... *Procris latifolia*

3a. Leaf margin entire or sometimes slightly toothed or wavy near apex 4
3b. Leaf margin toothed (dentate, serrate or crenate) .... *Procris frutescens*

4a. Leaves (megaphylls) ovate; venation asymmetric, 2- or 3-plinerved, secondary veins faint but usually distinct; petiole hairy .... *Procris acaulis*
4b. Leaves (megaphylls) oblong-elliptic; venation symmetric, pinnate, secondary veins inconspicuous; petiole glabrous .... *Procris pedunculata*

5a. Nanophylls present and persistent; leaf (megaphyll) broadly ovate; margin with rounded teeth; venation actinodromus; male inflorescence openly branched .... *Procris repens*
5b. Nanophylls absent; leaf (megaphyll) narrowly ovate-elliptic; margin obscurely toothed; venation pinnate; male inflorescence more or less compact with closed branching .... *Procris curtisii*

Note. The synonyms cited are only those that apply to Peninsular Malaysia.

1. *Procris acaulis* (Hook.f.) B.J.Conn & J.T.Hadiah, ***comb. nov.***
Basionym: *Pellionia acaulis* Hook.f., *Flora of British India* 5: 562 (1888). Synonyms: *Pellionia javanica* Wedd. var. *acaulis* (Hook.f.) Ridl., *J. Straits Br. Roy. Asiat. Soc.* 59: 187 (1911); *Elatostema latifolium* Blume var. *acaule* (Hook.f.) H.Schroeter, *Repert. Spec. Nov. Regni Veg. Beih.* 83(2): 17 & 1935 (1936). TYPE: Malaysia, Penang, on damp rocks, *King's Collectors 1659*, May 1881 (K).

Distribution. Peninsular Malaysia, Cambodia.

Selected specimens examined: PENINSULAR MALAYSIA. **Perak**: Temango, *Ridley 14560*, Jul 1909 (SING). **Penang**: refer Type above.

2. *Procris curtisii* (Ridl.) B.J.Conn & J.T.Hadiah, ***comb. nov.***
Basionym: *Pellionia curtisii* Ridl., *J. Straits Br. Roy. Asiat. Soc.* 82: 196 (1920). Synonym: *Elatostema curtisii* (Ridl.) H.Schroeter, *Repert. Spec. Nov. Regni Veg. Beih.* 83(2): 35 (1936). TYPE: Malaysia, Perak, Gunung Bajong, Malacca am Kantafluß, *Curtis s.n.*, Aug 1898 (SING).

Distribution. Peninsular Malaysia, Thailand, Philippines, Indonesia, Papua New Guinea, Solomon Islands.

Selected specimens examined: PENINSULAR MALAYSIA. **Perak**: Lenggong, *Ridley s.n.*, Aug 1909 (SING124283). **Selangor**: Gua Batu, *Ridley 4717*, 23 Jun 1889 (SING124284); *8196*, Dec 1898 (SING124286).

3. *Procris frutescens* Blume, *Bijdr.* 510 (1825–1826); H.Schroeter, *Repert. Spec. Nov. Regni Veg.* 45: 272 (1938), *descr. ampl.* TYPE: Indonesia, Java, *Blume 707*, without date (L).

Distribution. Peninsular Malaysia, Thailand, Philippines, Indonesia, Papua New Guinea, Solomon Islands.

Selected specimens examined: PENINSULAR MALAYSIA. **Perak**: Larut and Matang, Maxwell Hill, *Burkhill 12686*, 6 Mar 1924 (SING124847). **Kelantan**: Gua Musang, Batu Papan, *Kiew 2882 & Anthonysamy*, 9 May 1990 (SING124843). **Pahang**: Cameron Highlands, Boh Plantation, *Mohd Nur 32746*, 26 Apr 1937 (SING124838). **Johor**: Mawai–Jemaluang road, *Corner 32461*, 11 Oct 1936 (SING124839 & 124840).

4. *Procris latifolia* Blume, *Bijdr.* 10: 509 (1825).
Pellionia latifolia (Blume) Boerlage, *Handl.* 3: 375 (1900). *Elatostema latifolium* (Blume) H.Schroeter, *Repert. Spec. Nov. Regni Veg. Beih.* 83(2): 17 & 1935 (1936). TYPE: Indonesia, Java, Res. Bantam, Sadjira, *Blume s.n.* (B, BO, BRSL, L).
Pellionia helferiana Wedd., *Prodr. Syst. Nat. Regni Veg.* 16(1): 170 (1869); *Elatostema helferianum* (Wedd.) Hallier f., *Ann. Jard. Bot. Buitenzorg* 13: 316 (1896). TYPE: Andaman, *Helfer 4551* (K).
Pellionia javanica Wedd., *Arch. Mus. Hist. Nat.* 8: 288 (1856); *Elatostema javanicum* (Wedd.) Hallier f., *Ann. Jard. Bot. Buitenzorg* 13: 316 (1896). TYPE: Indonesia, Java, *Lobb 283*, *anno* 1846 (K, W).

Distribution. Peninsular Malaysia, Myanmar, Vietnam, Thailand, Indonesia.

Selected specimens examined: PENINSULAR MALAYSIA. **Kedah**: Langkawi, Selat Panchor *Henderson 29083*, 23 Nov 1934 (SING124292). **Penang**: Plant House no. 1, *Mohd Nur s.n.*, 23 Sep 1918 (SING124293); Balik Pulau, *Curtis 682*, Mar 1886 (K, SING124303 & 124304). **Perak**: Kuala Kangsar: Padang Rengas, *Burkill 13580*, 15 Jun 1924 (SING124295); Gunong Bubu, *Chew 1220*, 18 Aug 1966 (SING124298); Tapah, Jor, *Mohd Haniff 14253*, 15 Sep 1924 (SING124312). **Kelantan**: Gua Musang, *Henderson 22693*, 13 Aug 1929 (SING124307); *Henderson 19503*, 21 Oct 1927 (SING124311). **Selangor**: Kuala Lumpur, Batu Caves, *Teruya 498*, 20 Jan 1929

(SING124291); *Ridley 13370*, Aug 1900 (SING124322). **Pahang**: Tioman, Juara Bay, *Burkill s.n.*, Jun 1915 (SING124296 & 124297); Jerantut: Gunung Tahan, *Mohd Haniff 10197 & Mohd Nur*, 21 Jun 1922 (SING124314). **Malacca**: Bukit Naning, *Alvins 1105*, 26 Mar 1885 (SING124294). **Johor**: Gunung Sumalayang, *Chin 597*, 3 Feb 1971 (SING124300); Sungai Segun, *Corner 30694*, 10 Apr 1936 (SING124301 & 124302); Labis, Sungai Juasseh, *Mohd Shah 2287 & Ahmad*, 31 Jan 1971 (SING124317).

5. *Procris pedunculata* (J.R.Forst. & G.Forst.) Wedd., in DC. *Prodr.* 16: I, 191 (1869); H.Schroeter, *Repert. Spec. Nov. Regni Veg.* 45: 259, (1938) (emend., as *P. pedunculata* var. *eupedunculata*).
Basionym: *Elatostema pedunculata* J.R.Forst. & G.Forst., *Characteres Generum Plantarum*, 53 (1775). LECTOTYPE (designated by Smith 1981): Society Islands (Tahiti), *J.R. Forster s.n.*, (K; isolectotype MW).

Distribution. Peninsular Malaysia, Marquesas Islands, Philippines, Indonesia, Papua New Guinea, Solomon Islands, Christmas Islands; Cook Islands; Fiji; Society Islands.

Selected specimens examined: PENINSULAR MALAYSIA. **Perlis**: Titi Tinggi, Mata Ayer Forest Reserve, *Kiew 3702*, 1 Jul 1993 (SING124852). **Kelantan**: Gua Musang, *Kiew 2992*, 15 May 1990 (SING124851).

6. *Procris repens* (Lour.) B.J.Conn & J.T.Hadiah, ***comb. nov.***
Basionym: *Polychroa repens* Lour., *Fl. Cochinchinensis* 2: 559 (1790). *Synonyms: Elatostema repens* (Lour.) Hallier f., *Ann. Jard. Bot. Buitenzorg* 13: 316. (1896); *Pellionia repens* (Lour.) Merr., *Lingnan Sci. J.* 6(4): 326 (1928). TYPE: unknown – taxonomic concept applied here is based on the amplified concept of Schröter & Winkler (1935).
Pellionia daveauana N.E.Br., *Gard. Chron.* 1880(2): 262 (1880). TYPE: Vietnam, Phugnoe, *G. Lebeuf s.n.*, without date (K).

Distribution. Peninsular Malaysia, Thailand, Philippines, Indonesia.

Notes. Schröter (in Schröter & Winkler 1935) recognised three varieties within '*Elatostema repens*'; however, the taxonomic status of these taxa have not been evaluated here.

Selected specimens examined: PENINSULAR MALAYSIA. **Perlis**: Gua Burma, *Kiew 3655*, 28 Jun 1993 (SING124791). **Kedah**: Baling, Kedah Peak, *Curtis s.n.*, without date (SING124785). **Penang**: *Curtis s.n.*, without date (SING124782–124784); Plant House no. 9, *Mohd Nur s.n.* 24 Sep 1918 (SING124798). **Perak**: *Scortechini 485*, without date (K); Hulu Perak, Grik, *Burkill 12545 & Mohd Haniff*, 19 Jun 1924 (SING124779); Kuala Kangsar, Kota Lama, *Mohd Haniff 15528*, 20 Oct 1924

(SING124796). **Kelantan**: Gua Ninik, *Henderson 19690*, 26 Oct 1927 (SING124788); Sungai Ketil, *Henderson 22665*, 12 Aug 1929 (SING124789); Sungai Bring, *Kiew 2904*, 11 May 1990 (SING124790). **Selangor**: Gombak, Batu Caves, *Ridley 8186*, Dec 1896 (SING124800); Kepong, *Symington 25169*, 29 Jul 1931 (SING124806). **Pahang**: Bentong, *Burkill 16533 & Mohd Haniff*, 6 Nov 1924 (SING124777); Raub, Gali, *Burkill 16839 & Mohd Haniff*, 13 Nov 1924 (SING124778). **Negeri Sembilan**: Bukit Sutu, *Alvins 1962* 1 Nov 1885 (SING124775); Tampin, *Burkill 2515*, 14 Jul 1917 (SING124776).

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Towards a revision of *Lejeunea* (Lejeuneaceae) in Malaysia

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ABSTRACT. As currently delimited, *Lejeunea* Lib. is characterised by the hyaline papilla at the proximal side of the first tooth of the lobule; the usual absence of ocelli in the leaf lobe; lobules occasionally reduced and with a single tooth; small, finely granular or homogeneous oil bodies; underleaves without or with straight, upright lobes; thin-walled epidermal cells that are larger than the medullary cells; branches of the *Lejeunea*-type; and gynoecia with lejeuneoid innovations. In Malaysia, 29 species of *Lejeunea* have hitherto been recognised. In the framework of an ongoing taxonomic revision, all characters used to circumscribe the genus and the species from Malaysia have been critically assessed based on study of fresh material collected during many field excursions throughout Malaysia (the Peninsular, Sabah, Sarawak) as well as study of herbarium material. Some characters which were neglected previously, such as the morphology of the first lobule tooth, superior central cells and female bracts and bracteoles, are being critically evaluated. These characters may be useful for differentiating *Lejeunea* from closely related genera, whereas characters of oil bodies, the perianth, the lobule with a large disc cell, and underleaves with two large basal cells, are also useful for distinguishing some species within the genus.

Keywords. *Lejeunea*, Lejeuneaceae, liverworts, Malaysia, taxonomy

Introduction

The pantropical genus *Lejeunea* Lib. is one of the largest genera in the liverwort (Marchantiophyta) family Lejeuneaceae, containing some 150–200 species, almost half of which occur in tropical Asia. The definition of the genus has long been problematic and many species currently placed in *Lejeunea* were previously assigned to other genera. It is also one of the most difficult and poorly understood hepatic genera. Species of *Lejeunea* are small to medium-sized plants, delicate, translucent, with shiny leaves in the field, frequently growing closely appressed on bark, living leaves and other substrates. The highly variable species *L. flava* has an almost worldwide distribution, occurring in Europe, North and South America, Africa, China, Japan, Indomalesia, Australasia and the Pacific region, while other species are restricted only to Asia, Europe, Africa or the Americas.

In Malaysia, 29 species of *Lejeunea* have been reported, most of them from Mount Kinabalu with 26 recorded species (Eifrig 1937; Mizutani 1963, 1966, 1970, 1978; Kodama 1976; Lee et al. 2010a). Eleven species are recorded from Peninsular Malaysia, viz., *L. anisophylla* Mont. [= *L. borneensis Steph.*] (Kitagawa 1971), *L. flava* (Sw.) Nees, *L. patersonii* (Steph.) Steph., *L. cucullifiora (*Steph.) Mizut. [=*Taxilejeunea cucullifiora* Steph.], *L. albescens* (Steph.) Mizut. [= *Taxilejeunea albescens* Steph.] (Inoue 1967), *L. lumbricoides* (Nees) Nees, *L. umbilicata* (Nees) Nees (Tixier 1980), and *L. patriciae* Schäf.-Verw. (= *L. pilifera* Tixier) (Schäfer-Verwimp 2001), *L. discreta, L. eifrigii,* and *L. sordida* (Lee et al. 2010b). A revision of the genus *Lejeunea* in Malaysia is currently being undertaken at Universiti Kebangsaan Malaysia by the first author, based on examination of herbarium materials collected from this country, mainly by Mizutani in the twentieth century (Mizutani 1966), and also specimens from other herbaria such as SING, BOHR, HIRO, BO, CAL as well as fresh materials collected by the first author. Named specimens from adjacent countries are being compared with the Malaysian taxa. Approximately 500 samples, including most of the type specimens of *Lejeunea* occurring in this country, have so far been examined. The type specimens are from the Conservatoire et Jardin botaniques de la Ville de Genève (G), Switzerland, Herbarium Haussknecht (JE), Germany, and the Hattori Botanical Laboratory (NICH), Japan.

Characters delimiting the genus

Characters that differentiate the genus *Lejeunea* from others include the hyaline papilla at the proximal side of the first tooth of the lobule; the usual absence of ocelli; small, finely granular or homogeneous oil bodies; occasionally reduced lobules with one tooth; underleaves that are entire or with 2 straight, upright lobes; branches of the *Lejeunea*-type; and gynoecia with lejeuneoid innovations. Furthermore, there are some additional characters that appear to be useful in defining the genus and which were neglected previously, such as the morphology of the first lobule tooth, superior central cells and female bracts and bracteoles.

First tooth. The first tooth in most species of *Lejeunea* is straight and the apex never acuminate (Fig.1). The position of first tooth is usually upward-pointing, sometimes pointing towards the stem or away from the stem. This character can be used to distinguish *Lejeunea* from other genera in Lejeuneaceae such as *Cheilolejeunea* (Spruce) Schiffn. and *Drepanolejeunea* (Spruce) Schiffn. where the first tooth is strongly falcate and the apex occasionally acuminate, but seldom straight. *Cheilolejeunea* may sometimes be confused in its habit with *Lejeunea*, especially in the field. The main characters that differentiate these two genera are the position of the hyaline papilla and the morphology of the oil bodies. However, the hyaline papilla is often collapsed and the oil bodies rapidly evaporated in dried material. Therefore, the above described difference in the shape of the first tooth may be used to separate these two genera, at

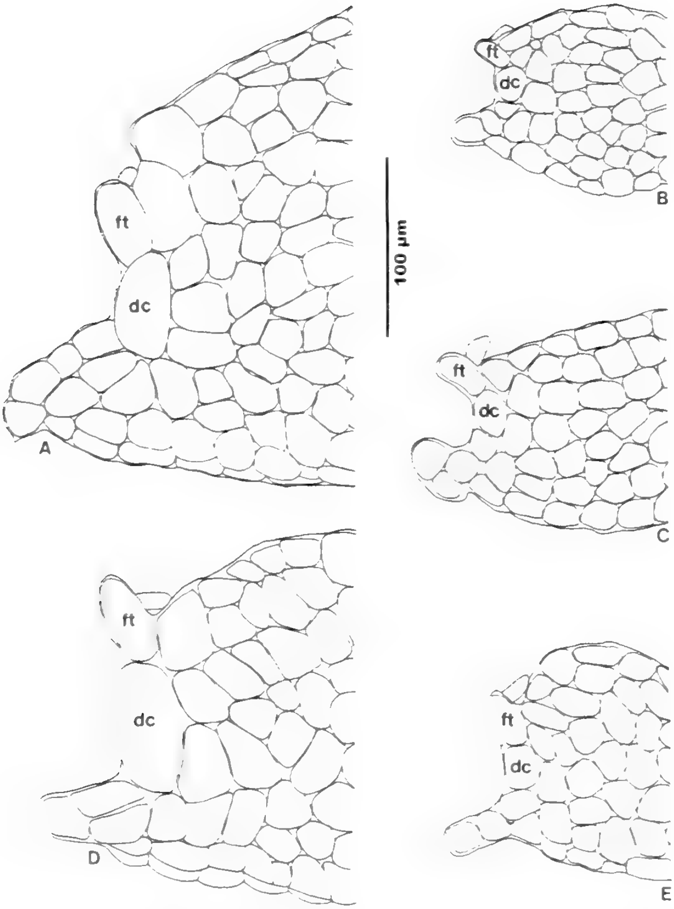

Fig. 1. Lobule apex in some Malaysian species of *Lejeunea* (hyaline papilla shown in gray). **A.** *L. discreta* Lindenb. from *Damanhuri s.n.* (UKMB). **B.** *L. microloba* Taylor from *Kodama 40783* (NICH). **C.** *L. sordida* (Nees) Nees from *G.E. Lee 1182* (UKMB). **D.** *L. lumbricoides* (Nees) Nees from *G.E. Lee 1155* (UKMB). **E.** *L. albescens* (Steph.) Mizut. from *G.E. Lee 1157* (UKMB). ft: first tooth, dc: disc cell.

least in Malaysia. The characters of the lobule tooth in Lejeuneaceae are discussed in detail by He (1996).

Superior central cells. The anatomy of the underleaf base has been discussed as a significant character in the taxonomy of the Lejeuneaceae (Bischler 1969, Winkler 1970, Gradstein 1975). The number of the superior central cells seems to be very constant at the genus level and taxonomically relevant (Gradstein 1975). The superior central cells can be perceived through transverse section of the underleaf base. The origin of the superior central cells remains uncertain (Gradstein 1975); according to Winkler (1970), they belong to the underleaf. According to Bischler (1969) and Winkler (1970), there are two superior central cells in the genera of Lejeuneoideae (including *Lejeunea*). However, our studies show the presence of 4 superior central cells in *L. lumbricoides* (Nees) Nees, *L. eifrigii* Mizut., *L. discreta* Lindenb. and *L. sordida* (Nees) Nees (Fig. 2). This character can distinguish some *Lejeunea* species from *Drepanolejeunea*, which has only two superior central cells (Gradstein 1975).

Female bracts and bracteoles. All the female bracts of *Lejeunea* have a rather short and straight keel, and always without any wing on the keel. The margin of the bracts and bracteoles are usually entire or slightly crenulate and seldom serrulate. The absence of winged bracts in *Lejeunea* can be used to separate *Microlejeunea* where the latter usually has winged or sinuate-dentate keels, with bracts and bracteoles occasionally dentate (Schuster 1980).

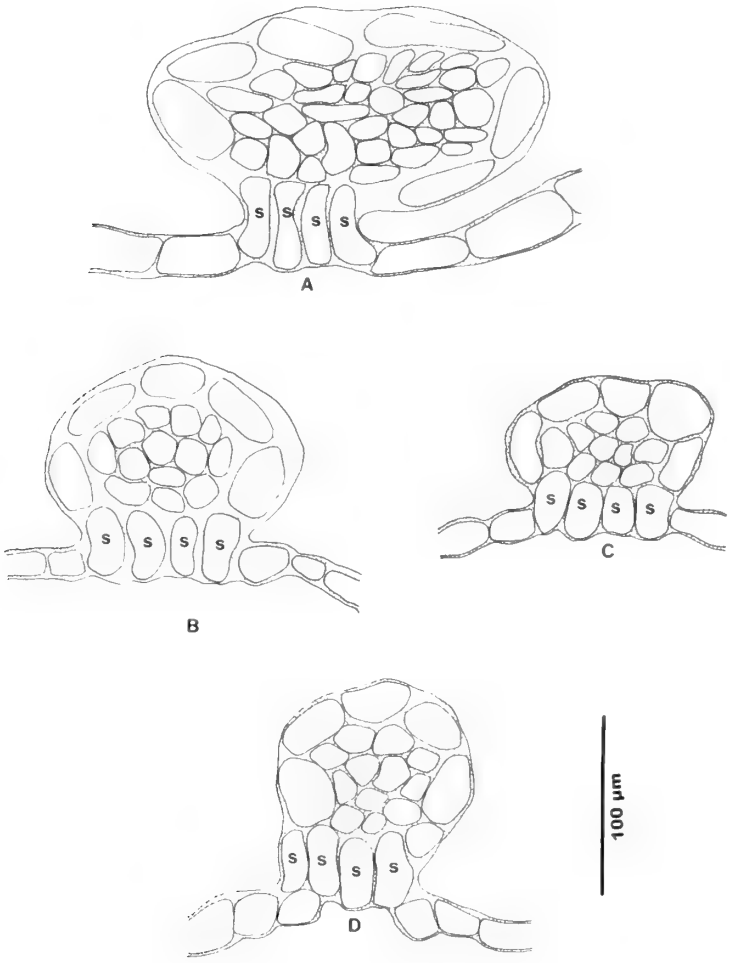

Fig. 2. Stem in cross section at the base of the underleaf, showing four superior central cells (s). **A.** *L. lumbricoides* (Nees) Nees from *G.E. Lee 1428* (UKMB). **B.** *L. discreta* Lindenb. from *Damanhuri s.n.* (UKMB). **C.** *L. sordida* (Nees) Nees from *G.E. Lee 1442* (UKMB). **D.** *L. eifrigii* Mizut. from *G.E. Lee 1194* (UKMB).

Characters in species delimitation

Leaf habit and shape. Most of the species of *Lejeunea* have flat leaves when moist, however some are with strongly convex leaves when moist, e.g., *L. pectinella* Mizut., *L. umbilicata* (Nees) Nees , *L. lumbricoides* (Nees) Nees, *L. contracta* Mizut. and *L. kinabalensis* Mizut. (Fig. 3). The convex leaf in the moist condition only seems to appear in more robust species of this genus. This character can be used to separate *L.*

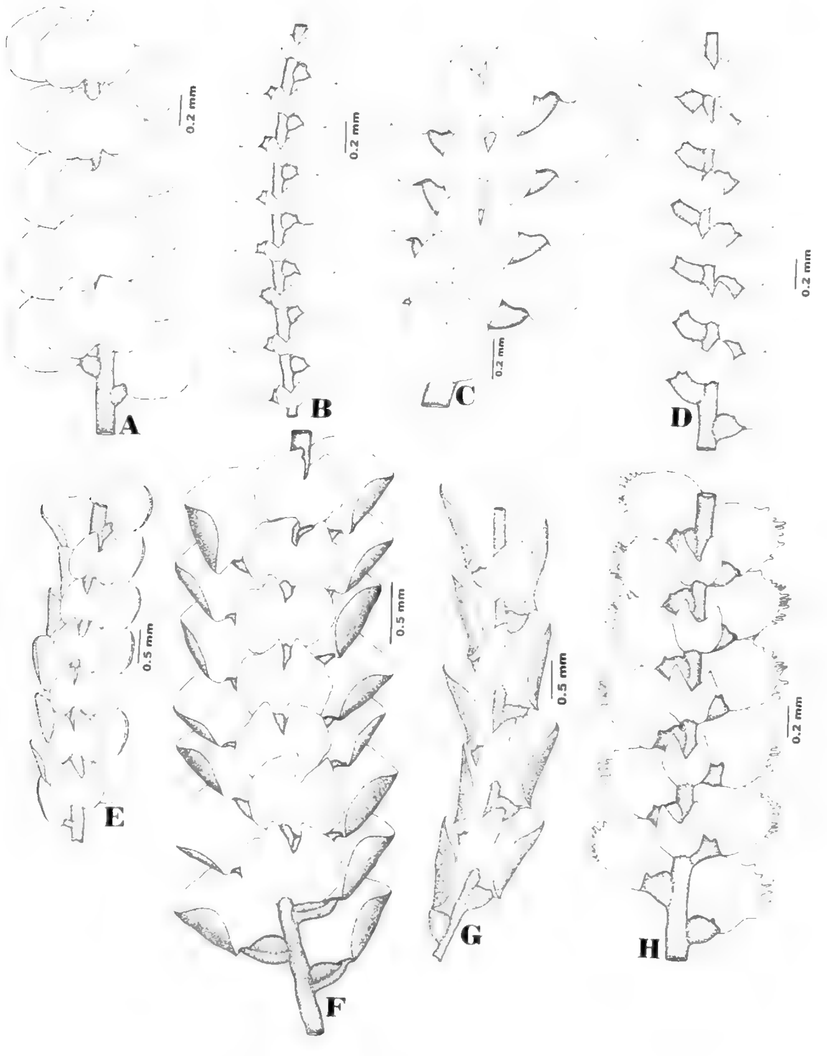

Fig. 3. Leaf habit and shape. **A.** *L. sordida* (Nees) Nees from *G.E. Lee 1154* (UKMB). **B.** *L. micholitzii* Mizut. from *Z. Iwatsuki 1383a* (NICH). **C.** *L. discreta* Lindenb. from *G.E. Lee 1146* (UKMB). **D.** *L. alata* Gott. from *G.E. Lee 1199* (UKMB). **E.** from the holotype of *L. kinabalensis* Mizut. (NICH). **F.** *L. pectinella* Mizut. from *G.E. Lee 1037* (UKMB). **G.** *L. lumbricoides* (Nees) Nees from *G.E. Lee 1155* (UKMB). **H.** *L. patriciae* Schäf.-Verw. from *G.E. Lee 1099* (UKMB).

pectinella Mizut. from *L. discreta* Lindenb., the former usually having convex leaves when moist (Fig. 3). Leaf shape in *Lejeunea* varies from narrowly to broadly ovate to rounded. The base is often gradually narrowed to the insertion which forms a long, J-shaped outline, along 10–15 cells. The apex is usually acute to rounded (Fig. 4), rarely apiculate except in *L. eifrigii* Mizut. and *L. microloba* Taylor, and without the marginal rhizoids as in *L. patriciae* Schäf.-Verw., which has leaves with 5–10 short rhizoids protruding from the apical margin.

Fig. 4. Leaf morphology. **A.** *L. sordida* (Nees) Nees from *G.E. Lee 1154* (UKMB). **B.** *L. pectinella* Mizut. from *G.E. Lee 1037* (UKMB). **C.** *L. wightii* Lindenb. from *G.E. Lee 1183* (UKMB). **D.** from the holotype of *L. kinabalensis* Mizut. (NICH). **E.** *L. anisophylla* Mont. from *G.E. Lee s.n.* (UKMB). **F.** *L. discreta* Lindenb. from *G.E. Lee 1146* (UKMB). **G.** *L. eifrigii* Mizut. from *G.E. Lee 1185* (UKMB). **H.** *L. patriciae* Schäf.-Verw. from *G.E. Lee 1099* (UKMB).

Oil bodies. Generally, *Lejeunea* has small, finely granular and homogenous oil bodies. The number of oil bodies per cell and the shape of the oil bodies varies among the species in this genus, e.g., *L. lumbricoides* (Nees) Nees has more than 8 oil bodies per cell, usually ovoid, rarely ellipsoid, slightly glistening, whereas *L. eifrigii* Mizut. has less than 8 oil bodies per cell, normally 3–5 per cell, usually ellipsoid, sometimes ovoid, and opaque (Fig. 5). However, most of the species, e.g., *L. discreta* Lindenb. and *L. patriciae* Schäf.-Verw. have more than 8 oil bodies per cell, ovoid to ellipsoid, which are glistening to somewhat opaque.

Perianth. The perianth in most species has 5 keels. However, perianths without keels can also be found as in *L. albescens* (Steph.) Mizut., *L. cucullifiora* (Steph.) Mizut., *L. microloba* Taylor and *L. umbilicata* (Nees) Nees. The eplicate perianth is rather a widespread character in *Lejeunea.* Reiner-Drehwald and Schäfer-Verwimp (2008) treated 13 species of *Lejeunea* with eplicate perianth, occurring in America, Europe

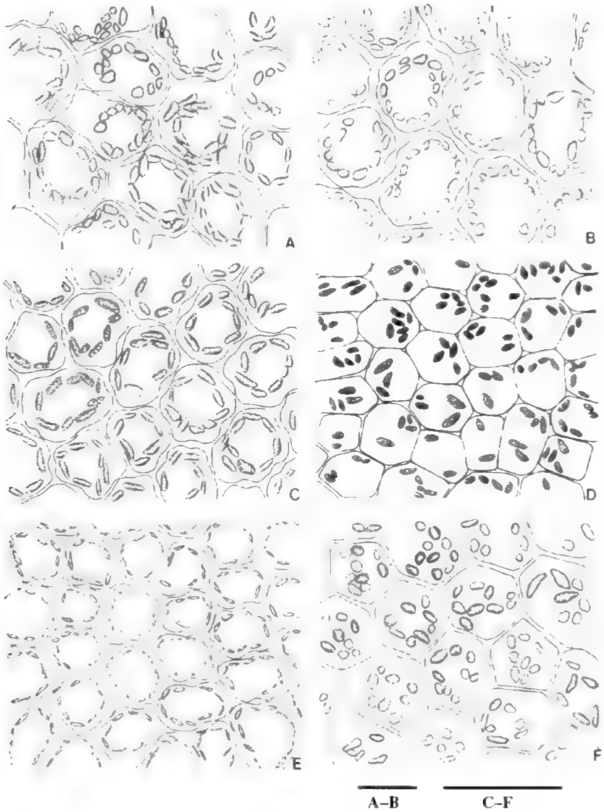

Fig. 5. Oil bodies. **A.** *L. patriciae* Schäf.-Verw. from *G.E. Lee 1099* (UKMB). **B.** *L. lumbricoides* (Nees) Nees from *G.E. Lee 1184* (UKMB). **C.** *L. discreta* Lindenb. from *G.E. Lee 1423* (UKMB). **D.** *L. eifrigii* Mizut. from *G.E. Lee 1194* (UKMB). **E.** *Lejeunea* sp. from *G.E. Lee 1424* (UKMB). **F.** *L. wightii* Lindenb. from *G.E. Lee 1423* (UKMB). Scale bars: A, B = 50 μm; C–F = 100 μm.

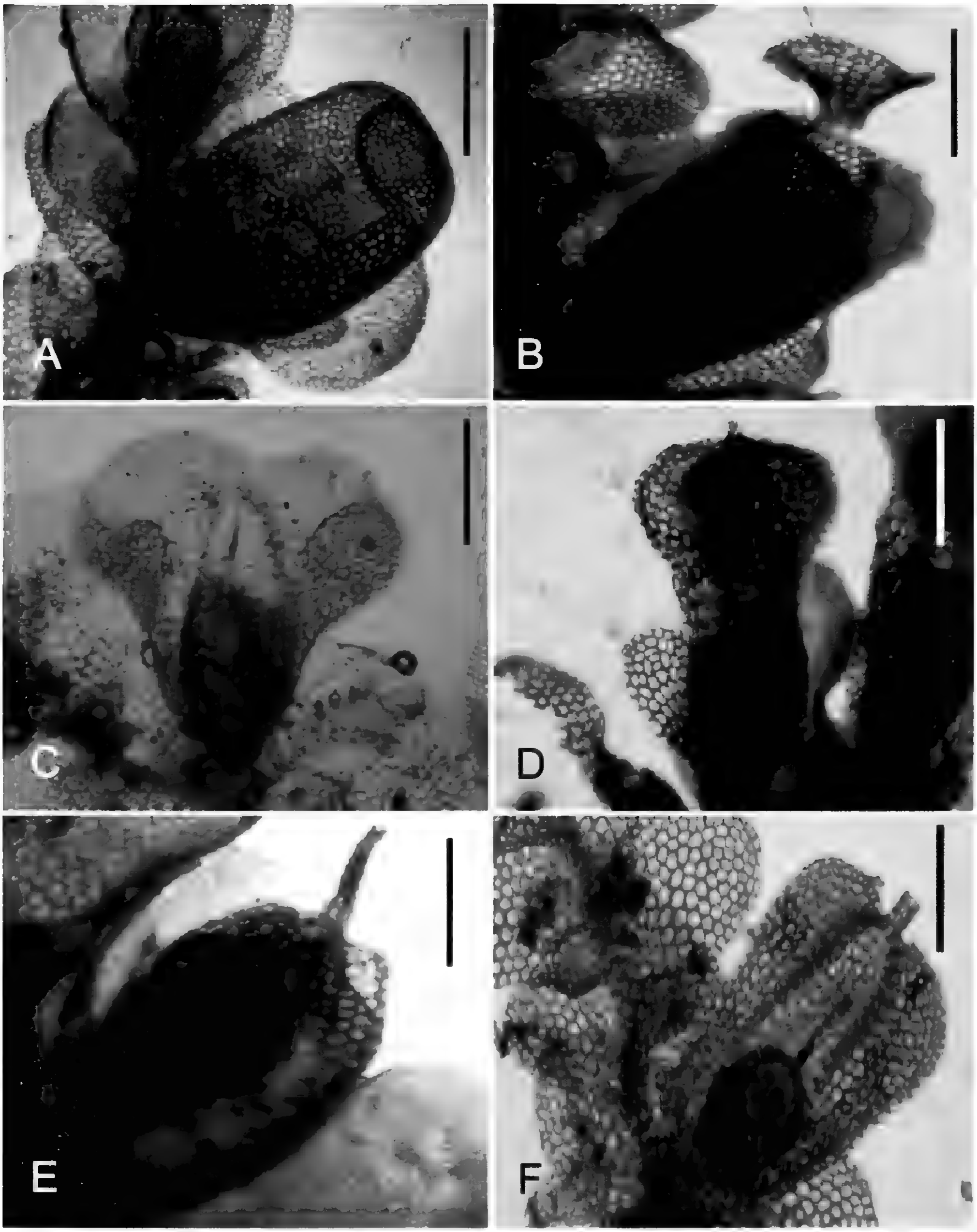

Fig. 6. The perianth of *Lejeunea*. **A.** *L. cuculliflora* (Steph.) Mizut. from *P.Y. Wong* with *Kim Wong 1604* (NICH). **B.** *L. mimula* Hürl. from *M. Mizutani 3239* (NICH). **C.** *L. papilionacea* Steph. from *Damanhuri s.n.* (UKMB). **D.** *L. eifrigii* Mizut. from *G.E. Lee 1185* (UKMB). **E.** *L. pectinella* from *Damanhuri s.n.* (UKMB). **F.** *L. anisophylla* Mont. from *G.E. Lee s.n.* (UKMB). Scale bars: A–F = 0.2 mm.

and Africa. The apex of the perianth also plays an important role in separating some of the taxa. A funnel-shaped apex is found only in *L. minuta* Hürl. and an apex with a 5–7-cells-long beak occurs only in *L. pectinella* Mizut. (Fig. 6).

Lobule with a large disc cell. In some species a large rectangular cell, called the disc cell by Mizutani (1970), very much larger than the first tooth, is situated below the first tooth (Fig. 1). Species with this peculiar character are *L. lumbricoides* (Nees) Nees and *L. discreta* Lindenb. Most species, however, lack such a large rectangular cell and sometimes this cell is of the same size as the first tooth, viz., in *L. albescens* (Steph.) Mizut., *L. microloba* Taylor, and *L. sordida* (Nees) Nees.

Underleaf with two large basal cells. This feature has been used to separate the species of *Lepidolejeunea* and *Luteolejeunea* by Piippo (1986). In the majority of *Lejeunea* species these two large basal cells are present and easily distinguished (Fig. 7). The presence of these two large basal cells was found in *L. lumbricoides* (Nees) Nees *L. microloba* Taylor, *L. umbilicata* (Nees) Nees and *L. eifrigii* Mizut. but not in *L. sordida* (Nees) Nees where the two large basal cells are undistinguishable.

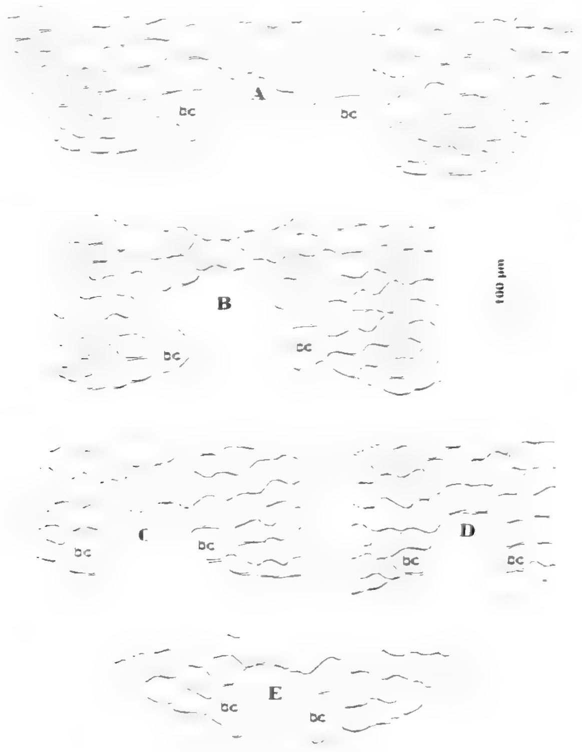

Fig. 7. Underleaf with two large basal cells (bc). **A.** *L. lumbricoides* (Nees) Nees from *G.E. Lee 1428* (UKMB). **B.** *L. microloba* Taylor from *Kodama 40783* (NICH). **C.** *L. umbilicata* (Nees) Nees from *M. Mizutani 3769* (NICH). **D.** *L. sordida* (Nees) Nees from *G.E. Lee 1231* (UKMB). **E.** *L. eifrigii* Mizut. from *G.E. Lee 1168* (UKMB).

Outlook

Our taxonomic study suggests that some species of *Lejeunea* are very similar and might lead to some new synonymy. For example, herbarium materials of *L. pectinella* Mizut. and *L. mizutanii* Grolle from Malaysia are very similar, *L. dipterocarpa* E.W. Jones from West Africa (Jones 1972), *L. hui* R.L. Zhu from China (Zhu & So 2001) and *L. kashyapii* M. Dey, D.K. Singh & D. Singh from India (Dey et al. 2008) are almost inseparable from *L. papilionacea* Steph. The last species was considered an African species but Söderström et al. (2010) have recently reported this species from Java where it was described as *Cardiolejeunea cadiantha* Schust. & Kachroo. If the above-mentioned species are indeed conspecific, it would seem that *L. papilionacea* Steph. is actually widespread in Asia. Furthermore, the difference between *L. wightii* Lindenb. and *L. tuberculosa* Steph., and between *L. cucullíflora* (Steph.) Mizut. and *L. umbilicata* (Nees) Nees, is probably not sufficient to warrant species distinction for these pairs of taxa. We are now trying to solve these problems by studying the type specimens and additional materials. We also expect that further new additions to Malaysia will be discovered in the future. Finally, we anticipate the separation of the genus *Microlejeunea* from *Lejeunea* and the treatment of the Asiatic *Lejeuna punctiformis* Taylor as a species of *Microlejeunea.* This species differs from *Lejeunea* species in the stem which has only 3 medullary cells in transverse section, leaf lobe with 1 or 2 ocelli at the base, a very large lobule, the first lobule tooth being rather long and curved, the keel of the female bracts winged and occasionally dentate female bracteoles. These characters also serve to separate *Microlejeunea* from *Lejeunea* (see, e.g., Bischler et al. (1962) for a thorough discussion of their differences).

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The study of larger basidiomycetes, especially polypores, in the Malesian region and the role of the Singapore Botanic Gardens

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ABSTRACT. The development of the study of larger basidiomycetes, especially polypores, in the Malesian region is presented. The historical importance of the botanical gardens in Bogor and Singapore is emphasised and an overview of the mycological collection in Singapore is given. This includes several isotypes of taxa described by G.E. Massee, C.G. Lloyd and N. Patouillard, as well as paratypes and holotypes of taxa described by E.J.H. Corner. The problems linked to Corner's material are discussed in the light of studies made in both Singapore and Edinburgh. The polypore collection in Singapore is a valuable resource for studying any geographical variation of fungal floras in the Malesian region and a unique tool for examining any temporal change in this flora, given the continuity of collections in the island since H.N. Ridley in 1892.

Keywords. Basidiomycetes, Malesia, polypores, Singapore Botanic Gardens

Introduction

The Malesian region in the sense of Flora Malesiana is one of the botanically most interesting tropical regions. Progress in the study of its vascular flora has been important but our knowledge of its mycological flora is still uneven, with some areas and some groups better sampled than others. The most intensively studied area is probably Peninsular Malaysia and Singapore and the best studied group is the larger basidiomycetes. This is linked to the work of E.J.H. Corner, based in Singapore in the thirties and forties. The importance of the mycological collection of the Singapore Botanic Gardens (SING, here and elsewhere, acronyms designing herbaria follow Holmgren et al. 1990) as well as that of E.J.H. Corner is emphasised. My experience is based on several stays in the Singapore Botanic Gardens and a recent one in the Royal Botanic Garden Edinburgh (E), the two institutions that host the majority of Corner's material. I also examined duplicates in the Royal Botanic Gardens Kew (K).

Mycology in the Malesian region

During the nineteenth and early twentieth centuries, mycological prospecting in the Malesian region was, except for some expeditions or cruises, centred on the two gardens linked to the British and Dutch presence in the region, Singapore and Bogor. However, no well-known specialist in mycology worked there until K.B. Boedijn arrived in Sumatra in 1926, moving in 1928 to the Bogor (then Buitenzorg) garden, and Corner in Singapore in 1929.

In mycological journals one will find biographies of those two scientists by Donk (1965) for Boedijn, and Watling (2001b) and Watling & Ginns (1998) for Corner. A detailed account of Corner's contribution to Malaysian mycology has been published by Watling in 2007.

Before the period of Boedijn and Corner, mycological collections were mostly made by general botanists and referred to overseas specialists. From the time of H.N. Ridley, directors or assistant directors of the Singapore Botanic Gardens have thus sent many collections to Kew, but also to N. Patouillard and especially C.G. Lloyd. The provided identifications form the basis of T.F. Chipp's catalogue of fungi of the Malay Peninsula (1921).

After the disruption of World War II, the situation diversified with more and more research performed in local institutions. This is especially the case at the Bogor herbarium with M. Rifai and the Forest Research Institute of Malaysia with S.S. Lee. In both institutions, young researchers are now active and mycology is really developing locally. This is accompanied by occasional involvement of foreign monographers, for whom the speed of air travel makes short visits to the tropics easier. The publication of nicely illustrated popular books like those of Tan (1990), Pegler (1997) and Zainuddin et al. (2010) will certainly develop the interest of the general public for fungi.

The state of development can be found in publications like the recent book edited by Jones, Hyde & Vikineswary (2007), the paper by Ahmad (1986) and the *Checklist of literature on Malaysian macrofungi* by Lee et al., which is only available on the internet (www.chm.frim.gov.my/Checklist_final.pdf).

The Singapore Botanic Gardens, which has been pivotal in those developments, does not have at the moment a resident mycologist but gives excellent facilities to visitors and curates meticulously a large mycological herbarium. Its importance for the study of fungi in the Malaysian Region should be emphasised and will be the object of the following section.

The mycological collection of the Singapore Botanic Gardens (SING)

The oldest fungal material in the herbarium of the Singapore Botanic Gardens goes back to H.N. Ridley and dates as far back as 1892. After 1900 one sees collections by I.H. Burkill and his wife E.M. Burkill, C.F. Baker and especially T.F. Chipp. Local collectors were Kiah, Nur and Sappan. When he replaced Chipp, R.E. Holttum was also active in mycological collecting. He mostly left this activity to Corner when the latter joined the staff, but kept making collections until the early thirties.

Many of those collectors regularly sent part of their material to Kew and to C.G. Lloyd. Massee, Lloyd and Patouillard have all described new species on the basis of these collections. The holotypes are of course in the herbarium of the describing author (K for Massee, BPI for Lloyd, FH for Patouillard) but it is usually overlooked that the isotype kept in Singapore can be a large collection from which a relatively small part has been sent. This isotype can thus be precious for estimating the variability of the type collection or in case of loss or damage to the holotype, as one can judge from the illustrations of this paper.

An example of a work by Massee on Singapore fungi is his *Fungi exotici XVII* (1914), entirely devoted to a mailing from Mrs. Burkill, with the description of 17 new species. A paper entirely devoted to Singapore boletes by Patouillard & Baker (1918) describes 16 new species. Some are discussed by Singer (1981), who revised their holotypes and a full discussion with type analysis is done by Watling (2001a). An example of those species is *Boletus spinifer* Pat. & C.F.Baker, whose holotype was also studied in detail by Heinemann & Rammeloo (1982). They noted a difference in pores from the original description and synthesise the numerous discussions of this unusual fungus. None of the authors who discussed this species seem to have thought of revising Baker's isotype in SING (no. 0036203). This could give more insight into the variability of the collection on characters like the pores.

It was only during 1917 that Baker was assistant-director of the Singapore Botanic Gardens, before moving to the Philippines. His collaboration with Patouillard was nonetheless fruitful, for besides the boletes, Patouillard (1922) based two new species of polypores on material sent by Baker. For one, *Phellinus chaetoloma* Pat., the isotype (SFN 5409) is important, for the holotype at FH has been determined as *Phellinus contiguus* (Pers.:Fr.) Pat. by Ryvarden (1983), while the original description does not fit that species, the setal structures in the hymenium being described as obtuse. This was noted by Corner (1991, p. 119) who examined the Singapore isotype and determined it as a resupinate *Phellinus noxius* (Corner) G.Cunn. I concur with this determination. Corner suggested the specimens have been muddled. It would thus be interesting to compare the two parts of the collection to confirm this. If *Ph. chaetoloma* is really the same as *Ph. noxius*, it will be necessary to conserve this well known, phytopathologically important name against *Ph. chaetoloma*, as well as if necessary against *Ph. sublamaensis* Lloyd, which was considered as a prior name for *Ph. noxius* by Ryvarden (1989).

The second species was *Phaeolus iobaphus* Pat., the isotype of which is also worth detailed study. Here also there is a discrepancy between the original description, that gives the spores as smooth, and the description by Ryvarden, that gives them as finely asperulate. My preliminary impression is that the collection could be heterogeneous (at least the SING part) and that in this SING part the asperulate spores could be a contamination.

On the basis of his type examination, Ryvarden combined the epithet in *Wrightoporia*. It is not clear whether Corner (1989a, p. 121) did look at the type himself, or relied on Ryvarden's description, but he made a further combination in *Steccherícium*.

Several Singapore botanists, the last being R.E. Holttum, and the most prolific T.F. Chipp, have sent material, especially of polypores to C.G. Lloyd. Lloyd described several species on the basis of those collections, now housed in BPI. The polypore holotypes have been revised by Ryvarden (1989, 1990, 1992). The isotypes preserved in SING are however worthwhile studying for there can be a large collection of which a small part only was sent to Lloyd. Many collections which are not types are also interesting for understanding Lloyd's concepts and can be quite helpful for comparison when one is working in the Singapore herbarium (Fig. 1).

I did spot 18 isotypes of Lloyd's polypore species, some of which will be the object of separate publications. As an example (see also Fig. 2–4) of the interest of this material, I will discuss the case of *Hexagonia angulata* Lloyd and *H. umbrosa* Lloyd. The two species were published at a short interval in 1920 as follows: *H. umbrosa* Lloyd, Mycol. Writ. VI, Mycol. Not. 63 (May 1920) 957, with no figure; and *H. angulata* Lloyd, Mycol Writ. VI, Mycol. Not. 64 (Sept. 1920) 1003, fig. 1831.

The type of *H. umbrosa* was not explicitly cited in the original description, but the collection "Blakang Mati, 24 Dec. 1919. On dead mangrove below high tide mark, T.F. Chipp. Singapore Field Number 5460", present number 31697, is accompanied by a note by Lloyd "5460 Hexagona umbrosa. This is the second collection you have sent. The former was referred to Hexagona tenuis but this dark plant should have a name." This is a clear link to the publication, where it is stated: "This is the second collection of this dark umber plant received from Mr Chipp…"

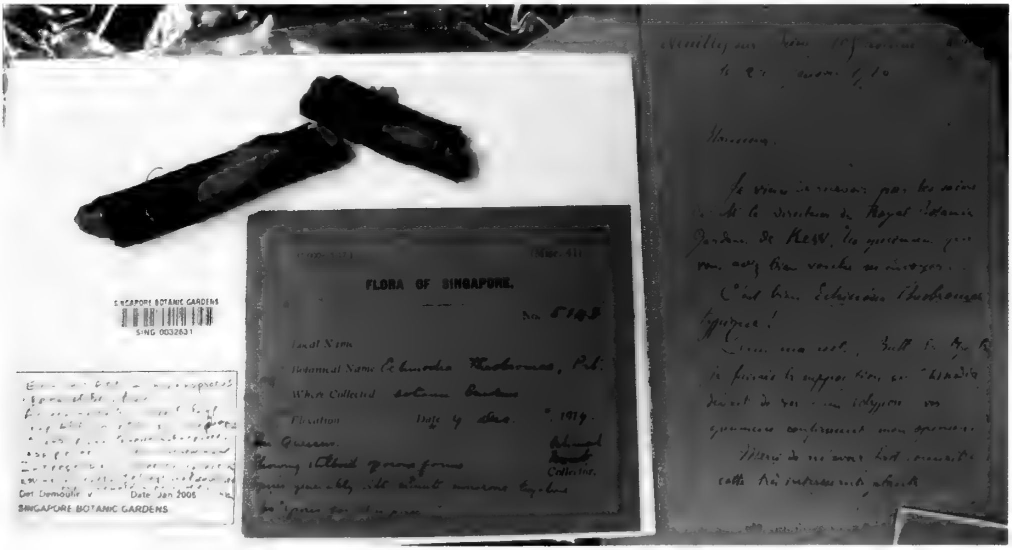

Fig. 1. *Echinoporia hydnophora* (Berk. et Broome) Ryvarden sub *Echinodia theobromae* Pat.. Singapore, Botanic Gardens, on *Quercus*, 9 Dec 1919, Ahmad, S.F.N. 5143, new number SING 32631, is an example of an important historical collection in the Singapore herbarium, even if not a type. Parts of this collection were sent by T.F. Chipp to Kew and to Lloyd. Patouillard got a piece through Kew and sent to Singapore the letter reproduced here. Lloyd also reported his comments (not reproduced here), which were published in Mycol. Writ. VI, Mycol. Not. 62 (Jan. 1920) 934–935, fig. 1704, 1705. This is the collection that convinced both Patouillard and Lloyd that *Echinodia theobromae* (a name with a complex nomenclature outside the scope of this paper) was indeed the conidial stage of a polypore.

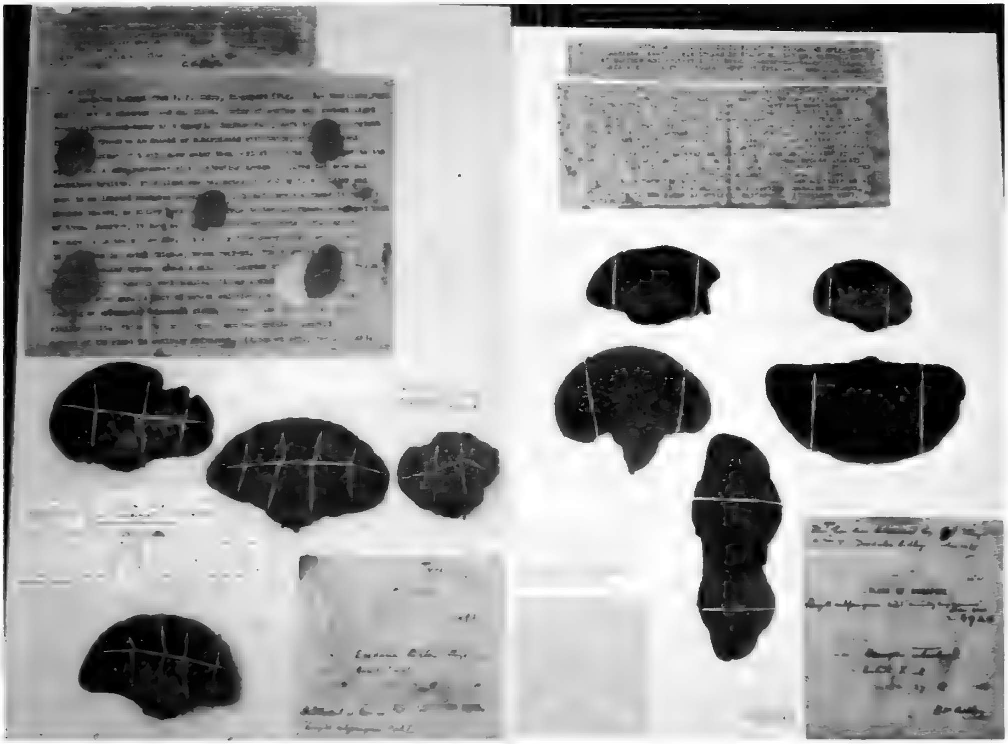

Fig. 2. Isotype of *Daedalea ridleyi* Lloyd, Mycol Writ. VI, Mycol. Not. 62 (Jan. 1920) 930, fig. 1689 at SING. The 10 fruitbodies have been mounted on two sheets. This is a single collection (Singapore, Bukit Timah, 27.8.1900, H.N. Ridley, S.F.N. 4920) but later the two sheets have been given different new numbers (31717 and 32628). One has been placed in the type collection and not the other. They should be reunited in the type collection and worth a detailed study. The holotype was identified "*Lenzites acuta* Berk." by Ryvarden (1989), but despite Lloyd's comment that it is not related, I believe it is *Daedalea sprucei* Berk. or the related (if distinct) *D. langkawiensis* Corner, of which the type is also present in SING.

The isotype of *H. angulata* was annotated "Pulau Penang, Waterfall Gardens, 23 jan. 1920, M. Noor, coffee brown on dead wood. Singapore Field Number 5604", present number 31696. It fits well the picture 1831 of Lloyd.

Those two collections were studied by Corner (1989a, pp. 20–21), while Ryvarden published his revision of the holotypes stored in BPI, in the same year.

Ryvarden placed the two names in synonymy with *Hexagonia tenuis* (Hook.) Fr., while Corner (1989b) synonymised *H. angulata* with *H. umbrosa*, which he considered distinct from *H. tenuis*, treated in *Trametes* (invalid publication).

I personally agree that the two collections belong to a single species, distinct from *H. tenuis* by being thicker and with bigger (about 1.5 mm) pores. I however do not consider the species as far away from *H. tenuis* as Corner thought. He gave great importance to the dimitic or trimitic nature of the context. There is however a large variation in the abundance of ramifications of thin hyphae, which already appears in Corner's description and I feel he overemphasised the character.

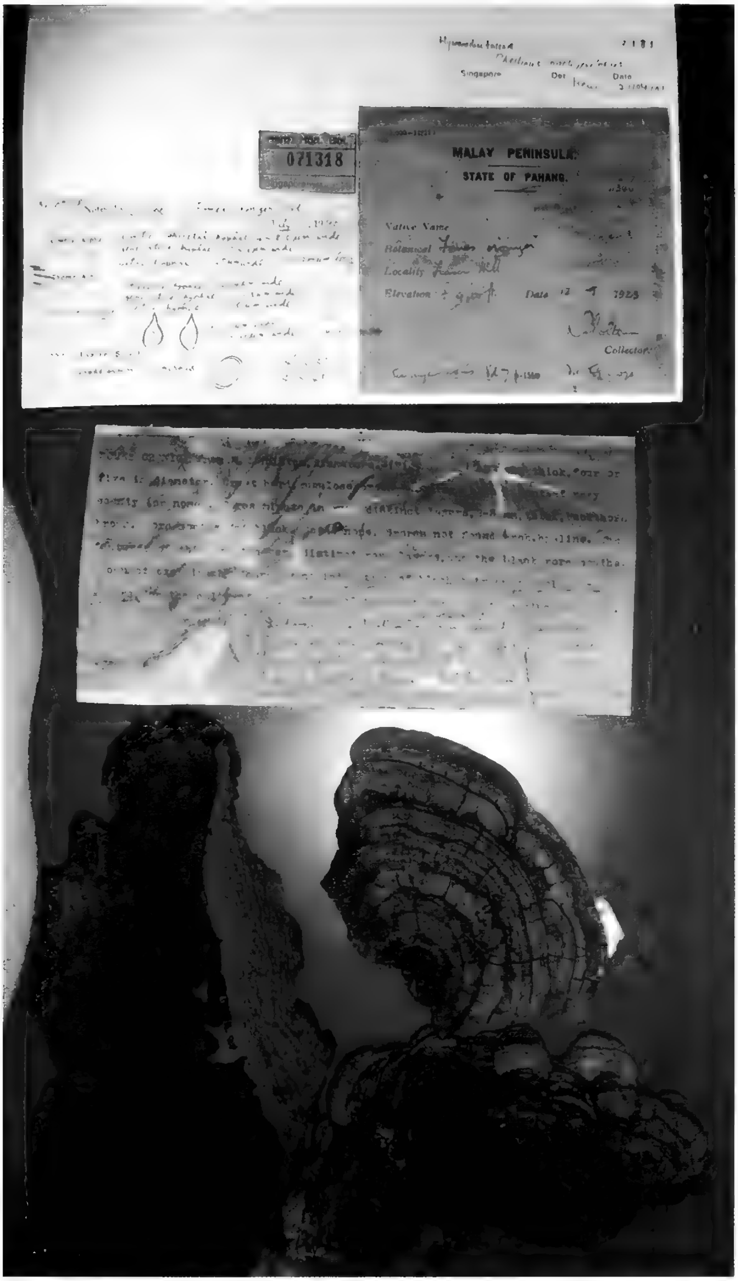

Fig. 3. Isotype of *Fomes oroniger* Lloyd, Mycol. Writ. VII, Mycol. Not. 73 (Oct 1924) 1330, fig. 3048 (with Note 74) at SING. Malay Peninsula, Pahang, Fraser Hill, Elev. about 4000 ft., 12.1.1923, R.E. Holttum, SFN 11346 (later renumbered 71318). Lloyd already relied on Holttum for the observation of the specimens retained in Singapore. The collection made up of three nice big fruitbodies was well annotated by Y. Abe in 1990, but I am not aware of a publication. The holotype was identified by Ryvarden (1989) as *Phellinus pachyphloeus* (Pat.) Pat., but the present isotype was cited as *Ph. melanodermus* (Pat.) Fidalgo by Corner (1991, p. 112), who uses different characters to differentiate the two species.

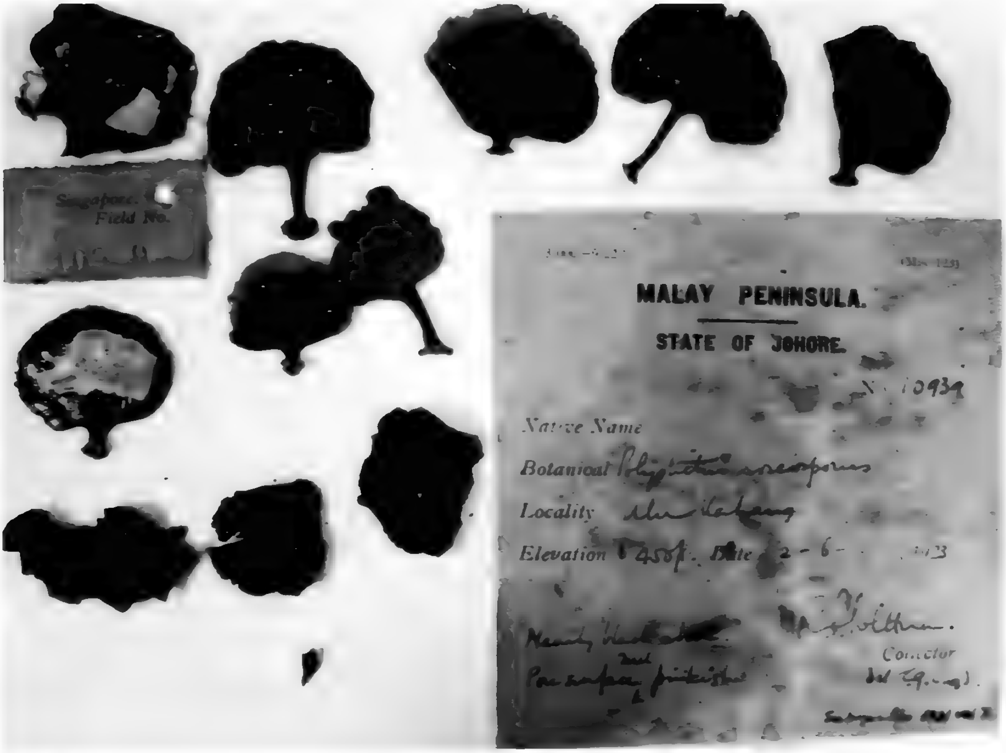

Fig. 4. Isotype of *Polystictus roseoporus* Lloyd, Mycol. Writ. VII, Mycol. Not. 73 (Oct 1924) 1331, fig. 3053 (with Note 74) at SING. Malay Peninsula. State of Johore. Ulu Kahang. Elev. 450 ft., 2.6.1923. R.E. Holttum. SFN 10939. The identity with *Microporus affinis* (Blume & Nees : Fr.) Kuntze proposed by Ryvarden (1992) after examination of the holotype is not problematic, but one can see the abundance and variability of specimens in the isotype.

A problem that however remains, is whether *H. umbrosa* is distinct from *H. umbrinella* Fr. The group of *H. tenuis* is certainly in need of revision and the well preserved isotypes at SING should be part of it.

Corner's mycological collections

As emphasised by Watling (especially 2007), intensive collecting by E.J.H. Corner has been fundamental in the study of mycological diversity in the Malesian region, as well as for mycological taxonomy as a whole.

Working with Corner's material is, however, not straightforward, as I have discovered after years of studies, initiated when R. Kiew, then curator of the Singapore herbarium, asked me to assess the significance of numerous collections stored in the Singapore herbarium, collections which had been overlooked for many years.

I concentrated my work on polypores, a group for which I had the necessary expertise, and especially well represented in the Singapore herbarium, which I visited several times from 2004 to 2010. At that time, the aim was to reorganise the polypore collection in an easily accessible way, made possible through two fellowships of the Singapore Botanic Gardens, with the support of the Belgian National Science Foundation (FNRS), as well as the general resources of my laboratory.

I have thus acquired a good idea of what material Corner had left in Singapore and could compare it to the material in his personal herbarium kept at the Royal Botanic Garden Edinburgh (E), as well as to the duplicates in Kew (K). Those visits to Great Britain were made possible by a grant for a sabbatical year made by the FNRS.

Most authors have taken for granted that Corner's types were systematically to be found in his personal herbarium at E, as if when leaving Singapore after the war, he had taken with him every interesting collection he had made. This is not the exact situation, and if it is true that a majority of types are now hosted in E, several paratypes and holotypes are to be found in SING. The great number of types kept in E makes the revision by Hattori, whose publication started in 2000, of foremost interest. My intention is to complement it with the Singapore types, through this paper and some subsequent ones.

That some holotypes of Corner's names should be in SING should be apparent to an attentive reader of his "Ad Polyporaceas" (1983–1991), where the mention "herb. Singapore" occurs beside the mention "herb. Corner".

It also happens that the institution or herbarium where the type is conserved was not indicated, and for types, this makes the new name invalid in the case of the Xanthochroic Polypores, Ad Polyporaceas VII. This last volume of the series was published in 1991, while Art. 37.7 of the ICBN (McNeill et al. 2006) makes such indication of the localisation of the type of a new name mandatory after 1990. An example of such an invalid name is *Phellinus glaucescens* (Petch) Ryvarden var. *minor* Corner (1991, p.93). If anybody wanted to validate that name, which is not my intention, the type is apparently the no. 28266 in SING, without corresponding material in E.

One should note that, despite its title, the publication by Corner in 1993, does not give indications on the status of its collections. It is a synthesis of the points of polypore taxonomy on which he disagreed with contemporary mycologists.

Most of Corner's collections in SING are from the years 1929–1932. This is, however, not exclusively so. There are collections from 1929 in E and from 1941 in SING. There is some difference in the proportion of material in E and SING by genera. I have only seen a single Corner collection of *Amauroderma* in SING (*A. rugosum*, Botanic gardens, 20/4/1932). This is not one of the ten bar-coded collections in E. The same situation occurs with *Trametes*, richly represented in E, but for which I have seen only three collections in SING. Those are of *Tr. persoonii* (Mont.) Pat. (later reduced to synonymy of *Tr. scabrosa* (Pers.) G. Cunn.), from 1929,1930 and 1941 and are not recorded in E.

In contrast, the Singapore herbarium is rich in *Phellinus*, under that name, or more often *Fomes*. It is in that genus that Corner described his first polypores in 1932. Those were:

- *Fomes levigatus* Corner, Trans. Br. Mycol. Soc. 17 (1932) 52. Later renamed *Phellinus leiomitus* Corner, Beih. Nova Hedwigia 101 (Ad Polyporaceas VII) (1991) 108, by reason of homonymy in the genus *Phellinus*.
- *Fomes senex* (Nees et Mont.) Imazeki var. *bulbosetosus* Corner, ibid.: 75.
- *Fomes senex* (Nees et Mont.) Imazeki var. *hamatus* Corner, ibid.: 75.
- *Fomes lamaensis* (Murrill) Pat. var. *secedens* Corner, Gard. Bull. Straits Settlem. 5 (1932) 341.
- *Fomes noxius* Corner, ibid.: 342.
- *Fomes pachyphloeus* Pat. var. *hispidus* Corner, ibid.: 347.

The holotypes of all these taxa are in SING (see, e.g., Fig. 5 and 6) and I have not located any material in E.

It may be that Corner had made enough progress in his study of *Phellinus* ("*Fomes*") not to consider it necessary to take much material with him when he left Singapore, especially given the fact that these are among the bulkiest polypores.

The type of *Phellinus noxius* (Corner) G.Cunn. is an especially noteworthy collection. It seems to have been split with one part placed in the type collection, receiving, in addition to the no. 25750, a general number 31727 (Fig. 6), while another part of 25750 is in the general herbarium, despite the mention in Corner's handwriting "Fomes noxius Corner. Type". The two parts should be reunited to better appreciate the variability of the collection. Indeed the type material is more dimidiate than one would guess from the original description. The importance of this collection comes from the possible conflict with previous, less well known names, like *Phellinus chaetoloma* Pat. and *Fomes sublamaensis* Lloyd. *Phellinus noxius* is a pathogen of major economic importance in the tropics, with 741 hits in Google Scholar, against 4 for *Ph. sublamaensis* (Lloyd) Ryvarden. Even if the synonymy with *Ph. sublamaensis* does not seem to be accepted anymore, *sublamaensis* being apparently a synonym of *Ph. lamaensis* (Murr.) Pat., conservation against *Ph. chaetoloma* might be necessary as stated earlier.

Corner has mostly used the collections he had made as types of his new names; however, he sometimes also used material of the Singapore herbarium collected by other people. For example, the holotype of *Inonotus perchocolatus* Corner, Beih. Nova Hedwigia 101 (Ad Polyporaceas VII) (1991) 123 was collected by Kiah. The holotype "Singapore, Dalvey Road, 14 May 1920, leg. Kiah, Sing. F.N. 5714" has received the new number 32830 and is what most authors would consider a *Phellinus* in need of further examination and not an *Inonotus*. In the same publication, p. 124, is also described a var. *parvisporus* of this species, with type "Malaya, Johore, leg. R.E. Holttum s.n. Jul. 1931; herb. Singapore (ut 'Poria 11a')". This is also present in SING and has received the number 28254, probably later than the study by Corner.

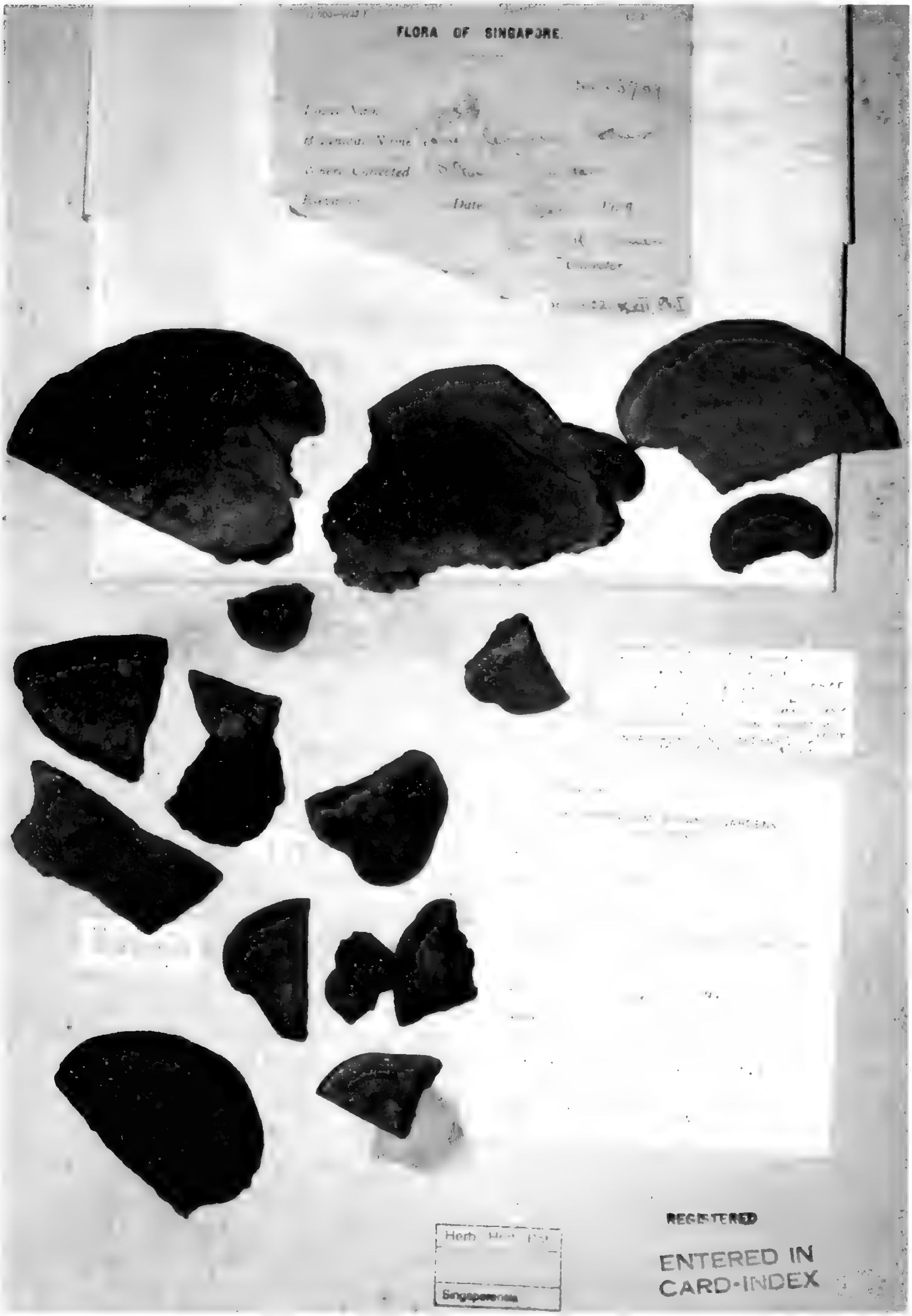

Fig. 5. Holotype of *Fomes levigatus* Corner, Trans. Br. Mycol. Soc. 17 (1932) 52 at SING, later renamed *Phellinus leiomitus* Corner, Beih. Nova Hedwigia 101 (1991), by reason of homonymy in the genus *Phellinus*. This taxon is usually ignored in recent treatments of *Phellinus*.

Fig. 6. Holotype of *Fomes noxius* Corner, Gard. Bull. Straits Settlem. 5 (1932) 341 at SING. *Phellinus noxius* (Corner) G.Cunn., a species of major phytopathological importance in the tropics. This is the part of the collection SFN 25750 which has received the new number 31727 and has been incorporated in the type collection. Another part of this collection is still in the general herbarium.

Perspectives for the future

Further developments in the study of the fungal flora of the Malesian region will certainly take place in several centres, especially the Bogor Herbarium and the Forest Research Institute Malaysia. For Singapore, interesting results will shortly come from the use of the rich herbarium.

The polypore collection in the Singapore herbarium, when reordered, will be an excellent tool for a model study of the fungal flora of the Malesian region. This is due to the large number of specimens that allow the study of the variability of species, and the presence of reference material, illuminating the concepts of authors like Lloyd and Corner.

It can be the basis of comparisons with distant areas, like Papua New Guinea, for which the Belgian herbaria GENT and LG hold numerous collections (Quanten 1997). This comparison would tell us if the polypore flora varies between the westernmost and easternmost parts of the Flora Malesiana territory.

It also presents a unique opportunity to follow floristic evolution in time. With areas like the Gardens' jungle or Bukit Timah regularly studied since Ridley's time at the end of the 19th century, one may get an indication of any change, linked to man's influence or climate, in the fungal flora of a tropical region. This, I believe, is unique in the world.

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e-Flora Malesiana: state of the art and perspectives

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ABSTRACT. An overview is presented of available e-taxonomic products and ongoing projects contributing to Flora Malesiana. This is presented in the context of a strong plea to strengthen the implementation of state-of-the-art e-taxonomy tools to speed up the generation and publication of Flora Malesiana information.

Keywords. EDIT, effective collaboration, European e-Floras Initiative, Flora Malesiana

Introduction

The increasing array of electronic taxonomy tools available for the elaboration and dissemination of floristic information has brought many advantages. It enables a shift from the traditional Flora concept as a static, printed account to a dynamic and interactive format, allowing for rapid updating and multiple uses of information. It provides taxonomists with means for instant interactive and remote co-operation, including continuous processes for evaluating preliminary results by peers and updating existing information. It also allows taxonomists to forge better links with their user-communities by making the products of their research more tailor made and accessible via internet (e.g., identification lists, specimen databases to monographs, biodiversity and Non-Timber Forest Products assessments, and analyses of spatial patterns of biodiversity).

In order to strengthen and speed up Flora Malesiana activities, Roos & Hovenkamp (2009) suggested that the Flora Malesiana community needed to adopt a more pragmatic and flexible attitude—flexible in terms of formats and publication strategy, and standards of robustness and confidence in the results.

The Flora Malesiana project has recently gained new momentum by starting a new website (www.floramalesiana.org), by adopting e-taxonomy tools and by joining a broadly supported initiative that wants to promote the adoption of richly interactive and truly collaborative systems for the production and presentation of floras: The European e-Floras (enhanced-Floras) initiative.

The European e-Floras initiative

Based on the results of an EDIT e-Flora Platform Workshop organised in Leiden (January 2010) the Board of the Foundation Flora Malesiana has decided during the most recent board meeting in Singapore to work towards an e-Flora Malesiana platform, to be developed in co-operation with the European e-Floras initiative. Participating institutions of the EDIT workshop in January also discussed the possibility of starting collaboration activities between Flora projects and the EDIT Platform for Cybertaxonomy by means of taxonomic exemplar groups (http://www.e-taxonomy.eu/node/748).

During a second workshop in Berlin (March 2010) three exemplary groups were set up: Flore d'Afrique centrale (National Botanic Garden of Belgium; Dessein et al., 2010; http://www.br.fgov.be/RESEARCH/DATABASES/FOCA/index.php), Flora Malesiana (Netherlands Centre for Biodiversity; http://160.45.63.201/dataportal/preview/flora-malesiana) and Kew's African Floras (Royal Botanic Gardens Kew).

During a third workshop organised in Brussels (September 2010) participants agreed to establish an "European e-Floras Initiative" to enhance communication between (e-)Flora authors, e-taxonomy initiatives and users of content and thus to increase research efficiency, reduce redundant efforts and speed up the preparation of up-to-date, high-quality content on plant biodiversity in formats permitting rapid updates and multiple uses (http://www.e-taxonomy.eu/node/859).

At present, the European e-Floras initiative is supported by 23 leading institutes from Europe, Asia, Africa and Australia involved in Flora production.

Why an e-Flora Malesiana?

The Flora Malesiana progress has lost some of its momentum since the beginning of the century. The overall progress in terms of the number of species covered is too slow (about 75% of all species in Malesiana still need to be treated) to make a meaningful contribution towards sustainability and conservation. Reasons for this are (i) the decreasing number of taxon experts that are available and devoted to write taxonomic treatments; (ii) the scattered generation of information and its particular usage (i.e., just for one specific project and format) in differently oriented projects; (iii) duplication of efforts; and (iv) different formats. In order to use the available expertise and resources effectively, a shift in the conventional work processes is needed.

Since 1950, Flora Malesiana has published its products as family treatments (in total 204 up to now). At present, several volumes are no longer available as hard copy (Series I Volume 1, 4–6, 9 Part 2–3 and Series II Volume 1 Part 1–3). Only the most recent volumes are available in electronic formats that can be more easily imported to a database than printed texts:

Text: Series I Volume 13;
Colour images: Volume 14;
Digital files: Volume 15 onwards, for Series II only Volume 3 completely available as digital files;
CD-ROMs: Leguminosae: Caesalpinioideae and Mimosoideae, Orchids of New Guinea Vol. I–VI, Orchids of the Philippines Vol. I.

An e-Flora will complement printed formats with electronic editions, offer unlimited access and instant updates, and increase the cost-effectiveness substantially by streamlining the production work flow. It will allow structured data entry, interactivity, multimedia, and enhanced accessibility. Moreover, it will also allow collaboration between several e-Flora projects (e.g., consortium members of the European e-Floras Initiative), users of taxonomic data, and other databases. This increases the possibilities for innovative scientific co-operation, also between other research fields (ecology, ethnobotany, etc.) and attracts worldwide contributors using services offered by the e-Flora.

How can FM work be strengthened?

Flora Malesiana (FM) work can be strengthened by increasing its global accessibility, facilitating efficient remote collaboration, making use of databases to safeguard data, changing the work flow in data preparation and presentation, and creating institutional commitment.

1. Increasing FM global accessibility

FM Website. The visibility of FM on the World Wide Web will be increased by bringing available information and data online via its website (www.floramalesiana.org). The current website will gradually be brought up to date both in design and contents, and will be established as the information exchange portal for FM.

It will feature information on the latest FM meetings (including web feed formats used to publish frequently updated works), and the FM Editorial Committee, collaborators, and other contributors. Furthermore, it will provide access to the FM e-Flora, and also include links to other relevant e-Floras, e-initiatives and or databases, e.g., Biodiversity Heritage Library (BHL), Cyclopedia of plant collectors, European Distributed Institute of Taxonomy (EDIT), Creating a Taxonomic e-Science (CATE), Journal Storage (JSTOR), specimen databases (e.g., plants.jstor.org), etc. FM printed volumes and CD-ROMs will be available through the website.

Interactive Key to the Malesian Seed Plants. The Interactive Key to the Malesian Seed Plants is a user-friendly electronic identification aid (DELTA key) for the plants in SE Asia. The first version was published on the web (www.kew.org/herbarium/keys/fm) and in CD-ROM format in 2004. It covers all seed plant families of the Malesian region, and is supported by c. 1000 pictures and family portraits. In the second version, the plan is to enlarge the key by including the plant families from Thailand and Indo-China, by including all genera done in the Flora Malesiana as possible answers, and by linking the key to the electronic version of the Flora.

List of remaining families. It is imperative that contributors and users can have access to available FM information and data. An inventory of the families still not allotted to (teams of) specialists and work that has been done and still needs to be done for Flora Malesiana (in terms of genera treatments) is being made available through the FM website. It will provide an overview of the different contributors, the working teams and the taxa they work on (with an indication how well verified or preliminary they are). The inventory will be periodically updated by the different contributors via the website contact (roos@nhn.leidenuniv.nl).

Checklist. For missing treatments a checklist of data will be made available by extracting the necessary data from the Kew World Checklist. This will form a backbone by incorporating missing parts of the FM area, provide an overview of missing taxa, connect information, and encourage people to start working on those taxa. It will also give an overview of the resources on the FM area that are still needed.

FM Bulletin. The FM Bulletin (http://www.nationaalherbarium.nl/fmbull/biblio.htm) contains the bibliography on Malesian botany, fieldwork and other field trips, etc. It was started in 1947 by C.G.G.J. van Steenis and through its indices is a goldmine of information on SE Asian floristics and taxonomy. At present the Bullletin has been reduced to the bibliographies on mosses and vascular plants and is only available online. These contain only the bibliographies published from volume 11 (6) 1995 to 2009, but not those of 13(4) through 14(3) as yet.

Cyclopedia of plant collectors. The Cyclopedia of plant collectors (http://www.nationaalherbarium.nl/fmcollectors) contains data on collectors in the Southeast Asian Archipelago, also known as Malesia (comprising Brunei, Indonesia, Malaysia, Papua New Guinea, Phillippines, Singapore, and Timor Leste). The data were collected by Mrs. Van Steenis-Kruseman and they are digitised from FM ser. 1, part 1, 5, and 8. Pictures of collectors and samples of handwriting and signatures are often included. The data on collecting trips are more or less complete up to 1974. Later data on collectors and their trips can be obtained from the FM Bulletin. The website is especially useful when one digitises hand written specimen labels from the earlier collectors.

2. *Facilitating efficient remote collaboration*

Collaboration can have different forms. A measure taken in 1989 to speed up and revitalise the FM project was to establish family teams. At present, the most common way is to divide work (either taxonomically or geographically), finish each part independently and perhaps build a common (set of linked) data base(s) (see, e.g., an early example, the Euphorbiaceae: www.nationaalherbarium.nl/euphorbs/) and compile an overall treatment at the end. However, to make full use of the e-possibilities, it is imperative to exploit the potential of internet communication tools that allow instant communication and sharing of data, such as online fora, Internet Relay Chat (IRC), Cloud computing services (e.g., Google Docs), and social networking tools, during the whole process of generating data and publishing information.

By making use of community e-tools for taxonomy (i.e., Scratchpads, EDIT Platform for Cybertaxonomy) the efficiency of the taxonomic work processes (data preparation and publication) could be increased. Scratchpads (http://scratchpads.eu) is a social networking application that enables communities of researchers to manage, share and publish taxonomic data online. It helps to increase visibility of ongoing projects, and creates interaction and synergy between remote working groups. The Taxonomic Editor - EDITor is part of the EDIT Platform for Cybertaxonomy (Berendsohn 2010). It is a desktop application that can be used to edit data stored in a standards-based community store (CDM-Store). It edits data in either a remote source, or a local data source embedded in the application. The EDITor allows collaborators to manage their data. Other CDM-based applications of the Platform allow the production of printed versions in flexible format or direct and up-date output to a website (CDM Data Portal). The latest version can be found at http://wp5.e-taxonomy.eu/cdm-setups/taxonomic_editor/).

3. *Making use of e-databases to safeguard FM data*

The defragmentation of taxonomic data and the use of common standards will increase the sustainability of FM work. The Common Data Model (CDM) is a data format for every conceivable type of data produced by taxonomists in the course of their work (http://wp5.e-taxonomy.eu/). It enables professionalised taxonomic software development and allows for common standards that create sustainability. Furthermore, it can be used to exchange information with other taxonomic databases such as BRAHMS (http://dps.plants.ox.ac.uk/bol/), and also non-taxonomic databases like TRY (http://www.try-db.org/). The CDM-based EDIT Platform for Cybertaxonomy will facilitate the generation of species lists without generic contradictions (with the advantage that other kinds of projects could also use it), but it also allows to store alternative taxonomic classifications, e.g. entire monographs and flora treatments. This will greatly assist the consolidation of the taxonomic research results in problem areas.

We envisage that the FM e-Flora will become available in several different formats: (i) for online use on personal computers and mobile phones; (ii) as stand-alone versions on CD/DVD-ROM or as down-loadable applications for smart phones, tablets, and other mobile devices; and (iii) as printed volumes using a print-on-demand system that will always use the latest version of the e-Flora.

4. Changing the work flow in data preparation and presentation

The use of e-tools facilitates the production of new content for printed and electronic publications (instead of using printed sources to produce digitised content). However, to port FM data, which is currently only available in print or in text format, to the online tools, markup is a prerequisite, i.e., the insertion of markers designating specific content types in the text (e.g., a generic name, a distribution record, etc.). FM floristic information is at present being digitised using XML (eXtensible Markup Language; see http://www.w3.org/standards/xml). FM volumes that are already available in a digital format can be marked up straightaway, whereas earlier volumes need to be scanned first in high quality.

Mark-up is generally performed in Microsoft Word, using a combination of automated procedures and manual corrections. Automation (e.g., Word-macros) may be used to speed up the mark-up process of highly structured texts. Manual corrections are required, e.g., when taxonomists have used various types of shorthand notations to combine similar species names into one paragraph in printed floras, or when typographical or text-recognition-errors interfere with the automated mark-up. The resulting XML-files are imported into the EDIT CDM using a specific import scheme. Figures are prepared for use with the marked-up files and the CDM, but are located on a separate image server. The mark-up process and preparation of the images takes roughly a month per volume to complete (25 MS pages/day). A preview of the future FM e-Flora portal as a CDM Dataportal implementation can be found at http://160.45.63.201/dataportal/preview/flora-malesiana. A finalised version of this portal will be made available through the FM website in 2011.

5. Creating institutional commitment

Institutional commitment from Flora Malesiana institutions and support of the European e-Floras Initiative activities is highly desirable and needed to speed up activities of the Flora Malesiana project. The institutional commitment that is necessary to achieve this is not limited to providing dedicated staff, but should also include the necessary infrastructure, including connections to available high-throughput internet facilities: TEIN3 and TEIN4 (http://www.tein3.net). Staff evaluation criteria should include also contributions towards data base maintenance, conforming to the recent MoU on Evaluation Criteria for Taxonomic Work as adopted by EDIT institutions.

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http://wp5.e-taxonomy.eu
http://www.br.fgov.be/RESEARCH/DATABASES/FOCA/index.php
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A summary of the total vascular plant flora of Singapore

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ABSTRACT. The last analysis of the vascular plant flora of Singapore was published more than a decade ago. Since then, the conservation statuses of all native species have been assessed and more exotic species have been recognised as naturalised. We present a holistic view of the family compositions and life forms of the total flora, including many exotic species that are found in cultivation only and not yet escaped or naturalised. Excluding extinct species, exotic species now outnumber native species. Horticultural introductions have also strongly influenced family compositions: legumes and palms are now the most species-rich families in the total flora. Legumes are also a dominant family among all naturalised life forms. We briefly discuss these implications for local conservation ecology.

Keywords. Cultivation, exotics, extinctions, natives, naturalisations, total flora, vascular plants

Introduction

Singapore's vascular plant flora is relatively well-documented for a tropical country. The first compilation was the *Flora of Singapore* by Ridley (1900) and his supplementary notes that shortly followed (Ridley 1901). The checklist by Turner et al. (1990) was the first, comprehensive, published update to Ridley (1900), and incorporated an unpublished Flora of Syonan compiled by the staff of the Singapore Botanic Gardens' Herbarium during the Japanese Occupation from 1942 to 1945, as well as Corlett's (1988) list of naturalised plant species. Turner et al.'s checklist was subsequently expanded into a fully-referenced list of vascular plant names (Turner 1993). Keng's (1973–1987) annotated lists of seed plants of Singapore were developed into the two volumes of the *Concise Flora of Singapore* (Keng 1990, Keng et al. 1998). These publications formed the backbone of subsequent updates and additions, and included native species, naturalised exotics, known escapes from cultivation and the most commonly cultivated species.

Two rounds of conservation assessments were conducted for the vascular plants and published as the first and second editions of the *Singapore Red Data Book* respectively (Ng & Wee 1994, Davison et al. 2008). With the second round of assessments, every native vascular plant species, with the exception of those few overlooked by past publications, has been assigned a conservation status. In addition, two editions of the *1001 Garden Plants in Singapore* (Boo et al. 2006) listed many more vascular plant species that are cultivated in Singapore. Although not a strictly botanical work, this book advanced our knowledge of the large numbers of plants that have been introduced into Singapore via horticulture. The chronology of these publications is summarised in a timeline in Fig. 1.

Although past work has already described the taxonomic composition and life-forms of the Singapore vascular plant flora, these have focused on various components such as the naturalised exotics (Corlett 1988) or the native species (Turner 1994, Turner et al. 1994). None of the studies, however, have taken a holistic approach to the floristic composition from a total flora perspective, i.e., one that takes into account all species found in the country, including exotics found in cultivation only.

We recently compiled a checklist of the total vascular plant flora of Singapore (Chong et al. 2009). In this paper, we summarise our findings on the taxonomic composition and life forms from a total flora perspective.

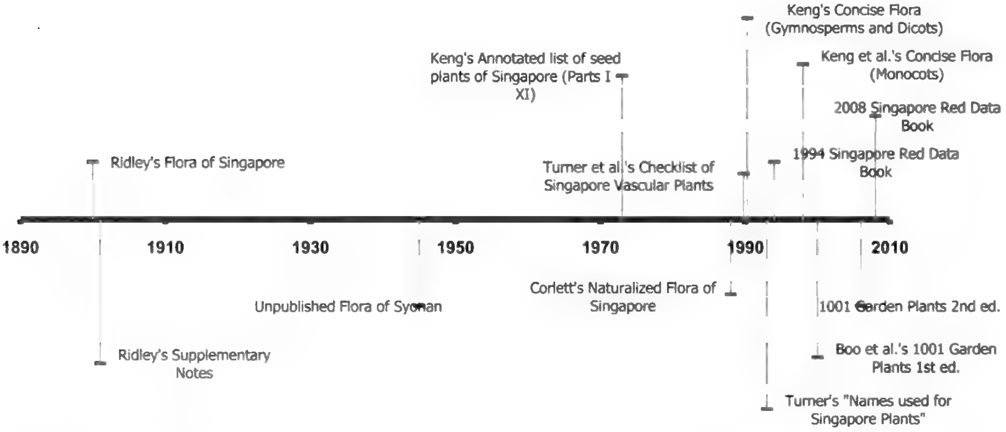

Fig. 1. Timeline of the major publications used in the compilation of a total flora of Singapore.

Materials and methods

Key reference sources and the methodology employed in the compilation of the flora used in this analysis is given in Chong et al. (2009). In summary, all plant names given in the local floristic literature reviewed above were compiled into a spreadsheet and checked for synonyms. Species that were inferred to have been present in Singapore before human-mediated introductions are considered "native". Native species that have not been collected or seen by botanists in the last 30 years are considered "extinct", as defined in Davison et al. (2008). Species whose presence is a result of human involvement are considered "exotic". Exotic species that have established outside of cultivation but rely on repeated introductions of propagules for persistence in the wild are termed "casual". Exotic species that maintain self-replacing populations in the wild independent of new human introductions are termed "naturalised". Remaining exotic species that can only be found in cultivation are termed "cultivated-only". For those weedy species that can only be found in human-modified habitats in Singapore, for which we lack knowledge of their original biogeographic range, we apply the term "cryptogenic" following the terminology by Carlton (1996).

Since the publication of our checklist, we have been continually updating and correcting our database upon encountering new literature and information provided by users of the checklist. Family circumscriptions of seed plants follow that of the Angiosperm Phylogeny Group (APGIII 2009, Stevens 2001 onwards), while non-seed plants follow Smith et al. (2006). The results presented here represent the most updated version of this database.

Results and discussion

In our checklist, we reported relative proportions of native, exotic and cryptogenic species. Here we report almost identical figures: there are 2141 native, 1822 exotic, and 210 cryptogenic species, constituting 51%, 44% and 5% of the total flora, respectively. The number of exotic species is an underestimate, as we are likely to have left out many other less commonly cultivated species in private gardens and nurseries.

Extinctions and introductions have had a major impact on the representation of families in the total flora (Table 1). The Orchidaceae was the largest native family, but massive extinctions, small numbers of species in cultivation and the absence of spontaneous exotics has reduced its rank to eighteenth in the total extant flora. The Rubiaceae, as the second largest native family, sustained far fewer extinctions and remains dominant as the largest extant native family and the third largest in the total extant flora. The Fabaceae is now the largest family overall as a result of high numbers of both spontaneous and cultivated exotics, followed by the Arecaceae, which has the largest number of cultivated species.

Trees are the most common life form for both natives and exotics (Fig. 2). Among the extant woody natives, the Rubiaceae are the largest family, with 17 extant tree species and 41 extant shrub species. These dominate the forest understorey. Among the native trees, the Meliaceae has sustained the largest number of extinctions (14 species; 35%), larger in proportion than other major families of trees. This may be attributed to the declines and extinctions of large frugivores that disperse the large-fruited Meliaceae, resulting in lack of recruitment and consequently decreased chances of population persistence (Corlett 2007).

Epiphytes are the only life form where most of the species have become extinct (Fig. 2a). Turner et al. (1994) noted that most of the epiphyte extinctions are accounted for by the epiphytic habit of the orchids, and that ferns, the second largest group of epiphytes, sustained proportionally far less extinctions. Here we repeat this observation but also show that the Apocynaceae and the Loranthaceae, the third and fourth largest families of epiphytes respectively, have suffered more than 50% extinctions (Table 2). The Apocynaceae epiphytes consist of only two genera: *Hoya* and *Dischidia*. The Loranthaceae consist solely of hemi-parasitic mistletoes. The susceptibility of epiphytes to extinction therefore appears to be consistent at least among flowering plant families.

Table 1. Largest 20 families in the vascular plant flora of Singapore. Ranks of 10 largest families within each category are given in superscript to the right of the number of species.

Family	All Natives	Extinct	Extant	Cryptogenic	All Exotics	Naturalised	Casual	Cultivated-only	All Wild	All Present
Fabaceae	61^{5}	11^{10}	50^{3}	8^{5}	190^{1}	46^{1}	10^{2}	134^{2}	104^{1}	248^{1}
Orchidaceae	226^{1}	181^{1}	45^{6}	1	7	0	1	6	46^{9}	53
Arecaceae	54^{9}	16^{5}	38	0	173^{2}	3	2	168^{1}	41	211^{2}
Rubiaceae	124^{2}	39^{2}	85^{1}	10^{4}	43^{9}	9^{5}	0	34^{10}	104^{1}	138^{3}
Poaceae	49	6	43^{7}	32^{2}	57^{5}	23^{2}	12^{1}	22	98^{3}	132^{4}
Myrtaceae	55^{8}	14^{7}	41^{9}	0	73^{3}	1	3^{8}	69^{3}	42	114^{5}
Apocynaceae	67^{3}	25^{3}	42^{8}	0	50^{7}	3	2	45^{6}	45^{10}	92^{6}
Cyperaceae	51^{10}	10	41^{9}	44^{1}	7	2	0	5	87^{4}	92^{6}
Malvaceae	37	6	31	7^{7}	54^{6}	3	4^{6}	47^{5}	41	92^{6}
Moraceae	60^{7}	10	50^{3}	1	31	1	7^{3}	23	52^{6}	82^{10}
Euphorbiaceae	48	12^{8}	36	4	39	10^{4}	3^{8}	26	50^{8}	79
Acanthaceae	16	5	11	6^{10}	66^{4}	6^{6}	4^{6}	56^{4}	23	83^{9}
Phyllanthaceae	61^{5}	12^{8}	49^{5}	0	16	3	1	12	52^{6}	65
Annonaceae	67^{3}	8	59^{2}	0	9	0	1	8	59^{5}	68
Araceae	30	2	28	4	41^{10}	5^{8}	6^{4}	30	37	73
Lamiaceae	23	9	14	7^{7}	39	5^{8}	5^{5}	29	26	60
Dipterocarpaceae	33	3	30	0	35	0	0	35^{8}	30	65
Asteraceae	6	1	5	14^{3}	45^{8}	16^{3}	3^{8}	26	35	64
Meliaceae	41	15^{6}	26	0	19	0	2	17	26	45
Melastomataceae	50	17^{4}	33	0	10	1	0	9	34	43

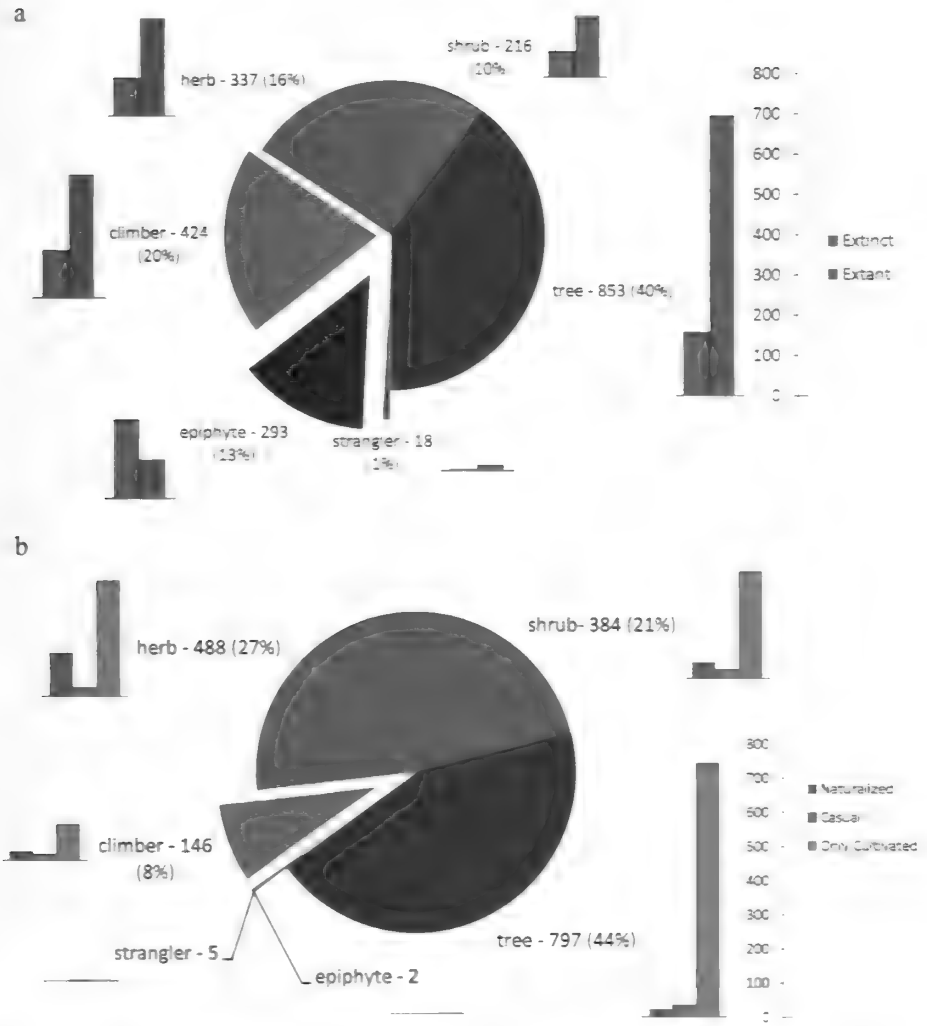

Fig. 2. Life forms of the (a) native and (b) exotic vascular plant species of Singapore.

Table 2. Largest five families of epiphytes in Singapore.

	No. of Epiphytic Species		
Family	All	Extinct	Extant
Orchidaceae	164	142	22
Polypodiaceae	19	3	16
Apocynaceae	17	9	8
Loranthaceae	14	8	6
Hymenophyllaceae	13	4	9

Of the exotic growth habits, the herbs have the largest proportion of naturalised species although more tree species were introduced for cultivation (Fig. 2b). Among the naturalised exotic species, the five largest families of climbers are Fabaceae (7 species), Convolvulaceae (4 species), Passifloraceae (3 species), Acanthaceae (2 species) and Cucurbitaceae (2 species). The five largest families for naturalised, non-climbing woody species are Fabaceae (29 species), Euphorbiaceae (5 species), Verbenaceae (5 species), Urticaceae (4 species) and Solanaceae (3 species). Finally, the 10 largest families of naturalised, non-climbing herbs are the Poaceae (23 species), Asteraceae (15 species), Fabaceae (10 species), Rubiaceae (8 species), Euphorbiaceae (5 species), Acanthaceae (4 species), Araceae (4 species), Amaranthaceae (4 species) and Cleomaceae (4 species). Many of these naturalised herbs are garden weeds or open wasteland ruderals and do not pose a threat to native forests. The woody naturalised species may be more of a cause for concern: some of the legumes form exotic-dominated woodlands where recruitment and regeneration of native species are slow, while other species such as *Cecropia pachystachya* Trécul (Urticaceae), *Ptychosperma macarthurii* (H.Wendl. ex H.J.Veitch.) H.Wendl. ex Hook.f. (Arecaceae) and *Syngonium podophyllum* Schott (Araceae) have been found in native forests edges and gaps (Lok et al. 2010).

Our compilation of a total vascular flora is the first for the tropics, and includes both the remnants of the original tropical rainforest cover as well as the elements of introduced flora from urbanisation. After taking extinctions into account, exotic species richness now exceeds native species richness. Considering that many of the native species are endangered and have small population sizes, while some exotic species have been planted in high densities throughout Singapore, the relative abundance of exotics to natives is also likely to reflect this. Although a large number of exotic species have been introduced, only a fraction has become naturalised, but more studies are needed to evaluate the impacts of these naturalisations on the local flora and fauna. Non-naturalised exotics in the urban environment also interact with native and exotic animals, providing nesting sites and food. Given the influence that cultivation can have on the floristic composition, replacing exotic horticultural species with native plants may be a strategy for conservation. Functional diversity lost from extinctions can be regained by reintroductions of extinct species, and populations of rare species can be augmented with horticultural plantings, while reducing the risks of invasive species introductions.

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The vegetation of Singapore —an updated map

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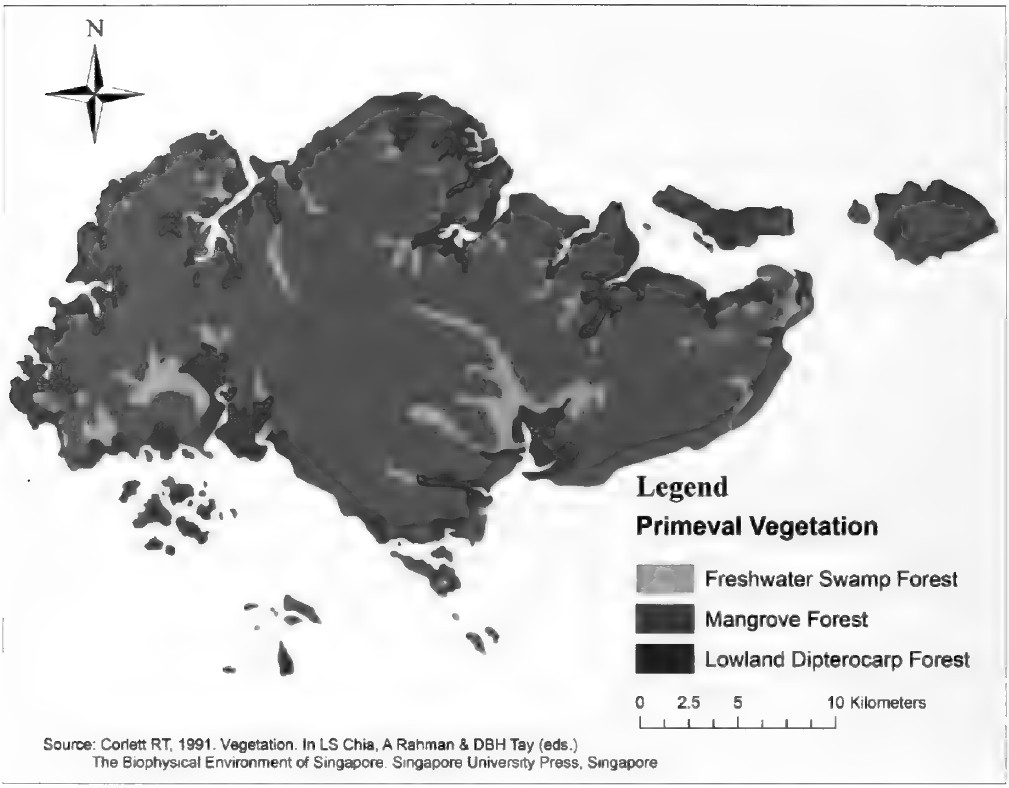
ABSTRACT. The primeval vegetation of Singapore was largely lowland dipterocarp forest, with mangrove forest lining much of the coast and freshwater swamp forest found further inland adjacent to the streams and rivers. After colonization by the British in 1819, almost all the primeval vegetation was cleared for agriculture and other land uses. The most comprehensive vegetation map of Singapore was made in the 1970s and has not been updated since. Here we present an updated vegetation map of Singapore using information from satellite images, published works, and extensive ground-truthing. Vegetation covers 56% of Singapore's total land area: 27% is actively managed (parks, gardens, lawns, etc.) and 29% is spontaneous vegetation. Primary lowland dipterocarp forest and freshwater swamp forest cover only 0.28% and is confined to the Bukit Timah and Central Catchment Nature Reserves. The majority of the non-managed vegetation is secondary forest of various kinds, dominated by native or alien trees. The managed vegetation and alien-dominated secondary vegetation are understudied and deserve more research attention. The vegetation of Singapore should be re-mapped at regular intervals in order to better understand the changes.

Keywords. Forest, map, Singapore, vegetation

Introduction

Most of primeval Singapore was covered by forest, while open habitats were largely confined to beaches and coastal cliffs (Corlett 1991, 1992a). According to Corlett (1991), 13% of the primeval vegetation was mangrove forest, 5% was freshwater swamp forest, and the rest was mainly lowland dipterocarp forest (Fig. 1). Although the island had been continuously inhabited for several centuries, rapid deforestation occurred only after colonization by the British in 1819. By 1900, 90% of the primeval forest had been cleared, mainly for agriculture and by 1935, rubber plantations occupied 40% of Singapore's area (Corlett 1991).

After the independence of Singapore in 1959, land use change was driven by urbanization and modernization. Active large-scale land reclamation has been carried out since the 1960s (Wong 1985). By 1973, less than 30% of Singapore's land area was covered by spontaneous vegetation while the rest was plantations, and suburban and



Source: Corlett RT, 1991. Vegetation. In LS Chia, A Rahman & DBH Tay (eds.)
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Fig. 1. Vegetation map of primeval Singapore.

urban areas (Hill 1977). By 1990, more than half of Singapore was urbanized, most of the plantations were abandoned and more than 99% of the original forest had been cleared (Corlett 1991, 1992a).

The vegetation of Singapore was partly mapped in the nineteenth century. For example, Coleman's and Thomson's maps showed vegetation around the Singapore Town (see Corlett 1992b). Vegetation can also be inferred from the topographic maps of Singapore. R.D. Hill (1977) produced the first extensive vegetation map based on aerial photographs from 1959 and 1969, and ground truthing from 1972 to 1973. Subsequently, only maps of specific areas or vegetation types were produced, such as the mangrove vegetation map of Hilton & Manning (1995), and the map of the vegetation of the Bukit Timah and Central Catchment Nature Reserves (see Corlett 1997). Therefore, we aim to produce a recent vegetation map for the entire Singapore.

Materials and methods

Ground truthing was carried out in Singapore from June 2009 to March 2010. The vegetation types were noted down in Singapore Street Directory, 2009 edition (Mighty Minds® 2009) if the area was bounded by roads, or in a GPS receiver (Garmin

GPSMAP® 60CSx) with at most ±7 m error if it was not bounded by roads. From the ground truthing data, 405 regions of interest (ROIs) were created.

Two SPOT 5 satellite images from 08 Mar. 2006 and 31 Aug. 2007, and the 405 ROIs were used to create a vegetation map of Singapore by a supervised classification technique, using the maximum likelihood method, which is available in the software package ENVI version 4.4 (ITT Visual Information Solution 2007). A total of 85 out of the 405 ROIs were used as the training data. The remaining 320 ROIs were used to assess the accuracy of the supervised classified vegetation map via the 'confusion matrix' function in ENVI version 4.4. Both satellite images underwent the same procedures. We adopted the standard of Thomson et al. (1999), which suggested at least 85% for overall accuracy, and at least 70% accuracy for individual classes.

When desirable accuracy was obtained (Tables 1 & 2), the supervised classified vegetation map based on the 31 Aug. 2007 satellite image was overlain with that based on the 08 Mar. 2006 satellite image (Fig. 2). Subsequently, persisting clouded areas were filled in using information from Google Earth 5.1.3533.1731 (Google Inc. 2009).

Table 1. Confusion matrix computed for the automated vegetation map of year 2006. Values are reported in percentages. The overall accuracy is 86.30%, and the Kappa coefficient is 0.7907.

	Ground truthed				
Supervised classification	Water	Non-vegetated	Grassland	Forest	Mangrove forest
Water	92.73	3.32	0.38	0.59	3.42
Non-vegetated	5.10	80.04	9.14	3.41	4.08
Grassland	0.12	12.49	75.28	6.81	0.02
Forest	1.82	3.63	15.15	88.33	11.15
Mangrove Forest	0.23	0.52	0.05	0.87	81.33

Table 2. Confusion matrix computed for the automated vegetation map of 2007. Values are reported in percentages. The overall accuracy is 90.61%, and the Kappa coefficient is 0.8621.

	Ground truthed				
Supervised classification	Water	Non-vegetated	Grassland	Forest	Mangrove forest
Water	97.43	0.08	0.08	0.00	1.60
Non-vegetated	2.40	88.09	7.99	0.59	3.08
Grassland	0.00	9.81	74.94	5.84	0.07
Forest	0.00	1.68	16.53	93.13	8.84
Mangrove Forest	0.17	0.35	0.46	0.45	86.41

Fig. 2. The final automated vegetation map of Singapore produced by filling in the clouded areas of the 2007 map with patches from the 2006 map.

The map was then overlain with layers showing the managed area in Singapore, and the Singapore Greenery Map (see Tee et al. 2009). Lastly, it was overlain with a layer showing areas of primary forest, old secondary forest, freshwater swamp forest, and mangrove forest, using information from personal communications and observations, the topographic map of Singapore (Singapore Mapping Unit 2006), the vegetation of the Bukit Timah and Central Catchment Nature Reserves (Corlett 1997), map of the freshwater swamp at Nee Soon (Tuner et al. 2006), and the mangrove vegetation of Singapore (Yee et al. 2010). As intermediate vegetation types exist, especially between young and old secondary forests, this study adopted a more conservative approach in classifying such vegetation. Hence, for example, forest that was intermediate between young and old secondary forest would be classified as young secondary forest.

Results and Discussion

Table 3 lists the spatial extent of each vegetation class and the updated vegetation map of Singapore is shown in Fig. 3. Vegetation covers 56% of Singapore's total land area. Actively managed vegetation occupies 27% of the total landmass while 29% of the area is covered by spontaneous vegetation, which includes scrubland, lowland forest, freshwater swamp forest, freshwater marsh, and mangrove forest. Primary forest only

Table 3. Area, proportion, and number of patches for each vegetation type. The total land area of Singapore taken here is 72,574.68 ha.

Vegetation types	Area (ha)	Proportion (%)	Number of patches
Non-vegetated	28,270.43	38.85	22275
Managed vegetation	19,972.96	27.45	29075
Scrubland	4,307.54	5.92	8340
Young secondary Forest	14,288.48	19.64	2920
Old secondary forest	994.68	1.37	42
Primary lowland dipterocarp forest	118.34	0.16	15
Mangrove forest	662.43	0.91	491
Freshwater marsh	76.6	0.11	227
Freshwater swamp forest	283.12	0.39	125

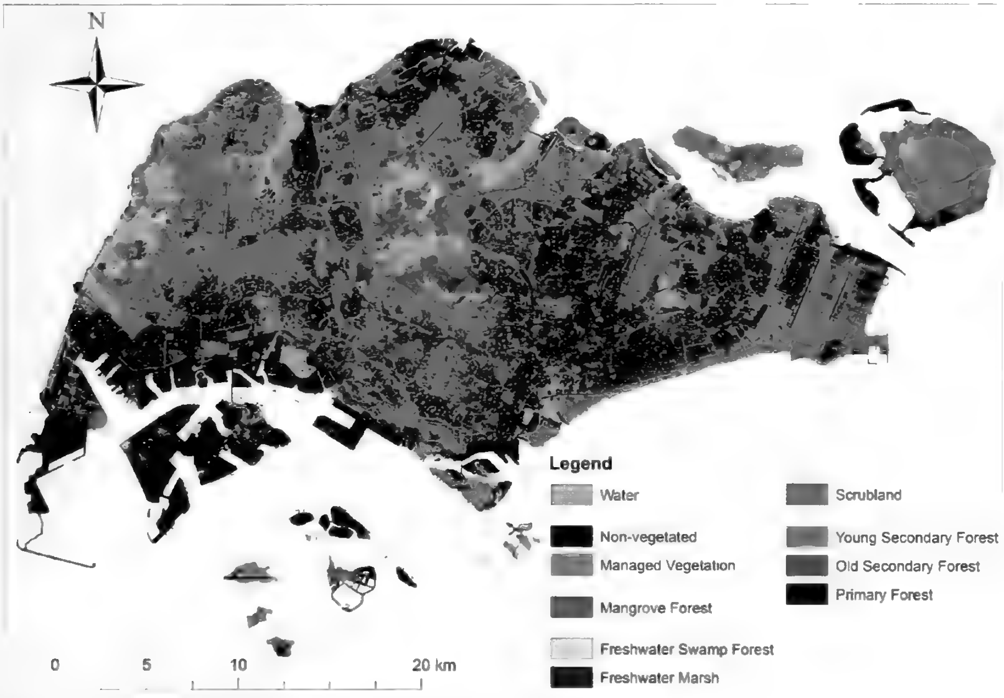

Fig. 3. The manually edited vegetation map of Singapore.

occupies 0.28% of Singapore's total landmass. A total of 118 ha of primary lowland dipterocarp forest can be found in the Bukit Timah Nature Reserve and in patches scattered throughout the Central Catchment Nature Reserve. Primary freshwater swamp forest, which is estimated to be 87 ha, can only be found in the Nee Soon swamp forest, which is located in the Central Catchment Nature Reserve (Turner et al. 1996).

Most of the spontaneous vegetation in Singapore belongs to lowland young secondary forest. The lowland young secondary forest can be further subdivided into native-dominated forest [e.g., young secondary forest dominated by *Adinandra dumosa* (Holttum 1954; Sim et al. 1992)], abandoned plantations, and open woodlands. However, these subtypes are not reflected in the map because they could only be poorly separated in the satellite images used. Moreover, extensive ground truthing in this forest type was not possible as some areas are inaccessible. Nonetheless, we observed that open woodlands, which are usually dominated by exotics like *Acacia auriculiformis* and *Leucaena leucocephala,* are common in recently cleared or reclaimed land. In the Nature Reserves in the centre of the island, native-dominated young secondary forests have been replaced through forest succession by taller, more species-rich, native-dominated old secondary forests (Corlett 1997), but the eventual fate of the exotic-dominated secondary forests outside the Reserves is unclear.

The ecology of managed vegetation in Singapore is also not well-understood, despite it constituting 48% of the total vegetation cover. As the major land use type in Singapore, managed vegetation has significant conservation potential and it has received increasing attention from the Singapore government lately. The planted trees can provide foods for birds and mammals. For example, the common palm civet (*Paradoxurus hermaphroditus*) has been found to feed on fruits of the rain tree (*Albizia saman*), the most widely planted street tree in Singapore (Xu 2010).

There are some limitations with the map. Firstly, it is based on satellite images from the years 2006 and 2007, but ground truthing was carried out in 2009 and 2010. This is likely to have affected the regions-of-interest (ROIs) drawn, hence affecting the supervised classification, and the accuracy of the map. Secondly, the maximum likelihood produces a hard (all or nothing) classification, assuming the whole pixel is homogenous. In reality pixels are rarely homogenous: for example, a pixel classified as forest might actually not be fully forested. Lastly, intermediate vegetation types exist, and this would once again affect the ROIs drawn. Despite these caveats, this map is still a good approximation to the vegetation of Singapore in 2006–2010. Fine-tuning could be done by using higher resolution satellite images and more ground truthing. We recommend a long-term follow-up study to document the changes in the vegetation of Singapore.

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Notes on Araceae of Kuala Koh, Kelantan, Peninsular Malaysia

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ABSTRACT. A total of 32 species from 11 genera of aroids were collected from Kuala Koh, Gua Musang, Kelantan. This represents about 23% out of an estimated 140 species and 39% of the 28 genera of aroids reported for Peninsular Malaysia. These include 24 species that are new records for Kelantan, including the recently described *Homalomena kualakohensis* Zulhazman, Mashhor & P.C.Boyce, and the very rare *Rhaphidophora corneri* P.C.Boyce, refound after 75 years.

Keywords. Araceae, checklist, Kelantan, Peninsular Malaysia

Introduction

The state of Kelantan is located in the northeast of Peninsular Malaysia and is fortunate to have remaining extensive areas of lowland forest and thus a rich and diverse lowland biodiversity, notably in the in the Kelantan delta. Together with extensive hill dipterocarp forests at Kuala Koh, the limestone hill and montane forests in south Kelantan and large water bodies at Pergau, resulting in a characteristic distribution of vegetation and especially composition and diversity of the aroids.

The earliest comprehensive account of the aroids of Peninsular Malaysia and Singapore is Hooker's Flora of British India (Hooker 1893), listing 89 species from 18 genera in Peninsular Malaysia. Thirty-two years later, Ridley (1925) conducted a comprehensive study on aroids of Peninsular Malaysia and recorded 123 species from 23 genera. The latest listing of aroids for Peninsular Malaysia (Mashhor et al. 2011) documents 140 species in 28 genera, which 25 species endemic. Studies on specific genera that relate to Peninsular Malaysia are those of Furtado (1939) on *Homalonema* Schott; Nicolson (1969) on *Aglaonema* Schott; Nicolson & Sivadasan (1981) on *Typhonium* (Schott); Hay (1996a) on *Colocasia* Schott; Boyce (1998) on *Epipremnum* Schott; Hay (1998) on *Alocasia* (Schott) G.Don; Boyce (1999) on *Rhaphidophora* Hassk; Nguyen & Boyce (1999) on *Amydrium* Schott; Hay (1996b) and Hay & Yuzammi (2000) on *Schismatoglottis* Zoll. & Moritzi; Bogner & Hay (2000) on *Piptospatha* N.E. Br.; Boyce & Hay (2001) on *Pothos* L.; Sofiman et al. (2009) on *Cryptocoryne* Fisch. ex Wydler., and Sofiman et al. (2010) on *Scindapsus* Schott.

To date, there is no comprehensive record of the species of Araceae in Kelantan. Previous studies on aroids related to Peninsular Malaysia, from Hooker (1893) and updated by Mashhor et al. (2011) showed that only 42 species from 15 genera recorded were collected from more than one location in Kelantan. Although there are a few surveys on plants in Kelantan, none has focussed specifically on aroids. For example, Chee et al. (2005) recorded just three species of aroids (*Algaomena nitidum* (Jack) Kunth, *Homalomena humilis* (Jack) Hook.f. and *Scindapsus scortechinii* Hook.f.) in their checklist survey on plant species of Gunung Stong Forest Reserve. Shamsul et al. (2005) also noted the same three species of aroids at different localities in the Gunung Stong Forest Reserve during their survey of seed plants. A recent survey by the first author of aroids in the granite area of the Jelawang Waterfall, Gunung Stong, revealed another novel species of aroid in Peninsular Malaysia, *Homalomena stongensis* Zulhazman, P.C.Boyce & Mashhor, ined. (Zulhazman et al. in press). The listing offered here is the first attempt to compile an inventory of the aroids for Kelantan.

Materials and methods

The study area is located in Kuala Koh at the southern part of Kelantan in the Gua Musang District, 180 km from the capital city of Kota Bharu. This area is covered with lowland moist perhumid dipterocarp forest at an average altitude of 100 m a.s.l. The surveyed area is at the confluence of two rivers, Sungai Lebir and Sungai Koh. Sungai Lebir is the main river that joins the Sungai Galas to the Sungai Kelantan at Kuala Krai.

Aroids were collected from Kuala Koh during field trips on 26–30 March and 31 May–2 June, 2010. Detailed samplings were made along a 3-km distance along the Rentis Ara. Specimens were collected with data on species identifications, habitats, elevation and location (longitude and altitude). The specimens were later brought to the Universiti Malaysia Kelantan and dried at 60°C. The dried material was processed as herbarium specimens and incorporated. The specimens were deposited to the Herbarium of Universiti Malaysia Kelantan, Malaysia. Appendix A shows the herbarium number for each specimen collected. The living specimens were planted at the Agro-Park, UMK as a pool genetic collection. The living collections are a vital resource for Araceae research. Access to a well curated living collection enables plants collected sterile to be flowered in cultivation. It facilitates crucially important enrichment of herbarium collections by enabling preparation of photographs and alcohol-preserved collections, etc. It also allows collection of fresh leaf samples for molecular data, and other materials for anatomical and developmental research.

Results and discussion

Thirty-two species from 11 genera of aroids were recorded from the study area. This represents about 23% of recorded species, and 39% of recorded genera for Peninsular

Malaysia. Appendix A lists the aroids recorded from Kuala Koh. This includes 24 species (75% of 32 species of aroids collected) which are new records for Kelantan, and one species new to science.

Six species of *Homolamena* Schott including one newly described species, *H. kualakohensis* Zulhazman, P.C.Boyce & Mashhor (Zulhazman et al. 2011) were recorded from this area. Other species are *H. pontederiifolia* Griff. ex Hook.f., *H. griffithii* (Schott) Hook.f., *H. wallichii* Schott., *H. rostrata* Griff. and an unidentified species of the Chamaecladon Supergroup.

Fifteen species from five genera of climbing aroids were collected from the area. *Rhaphidophora corneri* P.C.Boyce is one of the most remarkable species found at Kuala Koh (Boyce et al. in press). A small population of the species was located on sandy soil on ridge-tops and flat open areas. The Type and hitherto only known collection was collected by E.J.H. Corner in late 1935 from Kemaman, Terengganu (Boyce 1999).

A few aroid species were found to be significantly restricted to streams and associated gallery forests at Kuala Koh, as follows: *Schismatoglottis wallichii* Hook.f., *S. calyptrata* (Roxb.) Zoll. & Moritzi, *S. brevicuspis* Hook.f., *Apoballis brevipes* (Hook.f.) S.Y.Wong & P.C.Boyce and *A. mutata* (Hook.f.) S.Y.Wong & P.C.Boyce. *Scindapsus pictus* Hassk. was found on sloping and hilly areas. *Alocasia puber* (Hassk.) Schott, a species hitherto considered very rare in Peninsular Malaysia (Hay 1998) was noted to occur in inundated areas close to the stream.

Overall, most of the aroids found are restricted to the forest area, even though a few species such as the *Alocasia longiloba* Miq. Complex, *Amorphophallus prainii* Hook. f., and *Colocasia esculenta* (L.) Schott. can also be seen both within forest and in settlement areas. The last named is not native to Peninsular Malaysia. The most abundant species noted from this area is *Aglaonema nitidum* (Jack) Kunth. This species is distributed all over the area, especially on dry ridges.

Conclusions

This preliminary study lists 32 species in 11 genera of Araceae from the Kuala Koh, Kelantan. Among the collection, there are 24 species new for Kelantan and an undescribed species. The findings indicated that this area is relatively rich in aroids. The area should repay further study.

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Appendix A. List of aroids found in Kuala Koh, Gua Musang, Kelantan. E – endemic to Peninsular Malaysia; LC = Living collection; NR = new record for Kelantan; R = rare.

Genus	Species	Herbarium No.	Habitat	Remarks
Aglaonema	*nitidum* (Jack) Kunth	UMK 87	Dry ridges	
	simplex Blume	LC	Dry ridges	NR
Alocasia	*longiloba* Miq.	UMK 141	Ridges, open sites, dry spots, often within shrub areas	
	puber (Hassk.) Schott	UMK 139	Streambanks, wet sites	NR, R
Amorphophallus	*prainii* Hook.f.	LC	Dry ridges, often in shrub areas	NR
Amydrium	*medium* (Zoll. & Moritzi) Nicolson	UMK 92	Open canopy area, often on big trees	NR
Anadendrum	*microstachyum* de Ver & Becker	UMK 123	Shady wet areas, often on small trees	NR
Apoballis	*brevipes* (Hook.f.) S.Y. Wong & P.C. Boyce	UMK 110	Stream gallery, open areas	NR
	mutata (Hook.f.) S.Y. Wong & P.C. Boyce	UMK 104	Stream gallery, open areas	NR

Epipremnum	*giganteum* (Roxb.) Schott	UMK 128	Open canopy and dry areas, high ridges, often on big trees	NR
Homalomena	*griffithii* (Schott) Hook.f.	UMK 1	Slopes, ridges	
	pontederiifolia Griff. ex. Hook.f.	LC	Slopes, ridges	NR
	wallichii Schott	UMK 3	Slopes, ridges	NR
	rostrata Griff.	LC	Slopes, ridges	NR
	kualakohensis H. Zulhazman, M.Mashhor & P.C.Boyce	UMK 6	Slopes, ridges	NR, E
	Chamaecladon supergroup (Sp.1)	LC	Slopes, wet, stream margin, clay soil	NR
Rhaphidophora	*beccarii* (Engl.) Engl.	LC	Streambanks, on rock and soil, wet and shady area	
	corneri P.C.Boyce	UMK 31	Sandy soil, ridge-tops, flat open areas	NR, E
	falcata Ridl.	LC	Streambanks, on rock and soil, wet areas	NR
	korthalsii Schott	UMK 47	Shady wet areas, ridges, often on big trees	
	lobbii Schott	UMK 50	Shady wet areas, ridges, often on small trees	NR
	maingayi Hook.f.	UMK00033	Open canopy area, steep slopes, often on small trees	
Schismatoglottis	*brevicuspis* Hook.f.	LC	Streambanks, on wet and shady areas	NR
	calyptrata (Roxb.) Zoll. & Moritzi	UMK00059	On slopes, along the trail, shady area	
	scortechinii Hook.f.	UMK00056	Streambanks, slopes	NR, E
	wallichii Hook.f.	UMK00052	Stream gallery forests	
Scindapsus	*hederaceus* Schott	UMK00161	Open canopy areas, ridges, often on small trees, hemiepiphytic	NR
	perakensis Hook.f.	LC	Open areas, along trail, hemiepiphytic	NR
	pictus Hassk.	LC	On slopes, ridges, on soil and tree, surrounding with leaf litter	NR
	treubii Engl.	UMK00159	Shady areas, flat areas along trail, hemiepiphytic	NR
	sp.1	LC	Wet sites, hemiepiphytic	NR
	sp.2	LC	Half open canopy area, hemiepiphytic	NR

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Diversity and assessment of plants in Mt. Kitanglad Range Natural Park, Bukidnon, Southern Philippines

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ABSTRACT. This research describes the vegetation types, determines the diversity and assesses the conservation status of vascular plants in Mt. Kitanglad Range Natural Park, Bukidnon Province. Twelve 20 m × 20 m nested plots were established per vegetation type. A transect survey with 34 plots revealed three vegetation types, namely the agroecosystem, lower montane forest and mossy forest, with 661 species, 264 genera, and 106 families enumerated. Plant species richness and diversity decreases as the altitude increases, and the mossy forest had the lowest species diversity. *Lithocarpus sp.* obtained the highest Species Importance Value (SIV) for trees in both lower montane and mossy forests together, while *Leptospermum sp.* had the highest SIV in the mossy forest. Tree profile analysis showed that the lower montane forest had the highest mean number of species (7.9 spp.) and individuals (26.9 individuals), mean height (11.12 m) and mean diameter at breast height (dbh, 39.40 cm). The upper mossy forest had the lowest mean number of species (4.4 spp.), individuals (20.2 individuals), average height (7.03 m) and average dbh (16.60 cm). We assess 92 threatened and 82 rare species; 108 endemic species, 50 economically important species, 56 species newly recorded in the locality and 20 species newly recorded for the Philippines. Policy recommendations are given for protecting the remaining threatened, endemic and rare species of plants and their habitats.

Keywords. Conservation status, Mindanao, Mt. Kitanglad, Philippines, species diversity, vascular plants, vegetation types

Introduction

Mt. Kitanglad Range Natural Park has been declared as a protected area on November 9, 2000 and an ASEAN Heritage Park on October 29, 2009. Encompassing 37,236 ha over the North Central portion of Bukidnon and with the highest elevation of 2938 m, the park is the headwaters of three major river systems and sees frequent visitors (NORDECO 1998). Many faunal species were recorded in the park (Heaney et al. 2006, NORDECO 1998) but meager information is available about the richness and status of plants, especially at the northeastern part. It was therefore important that an inventory and assessment of the floral resources be conducted to generate knowledge on plant diversity and status for the conservation and protection of the remaining biodiversity. The findings of this research will be used as the basis for policy formulation by the Protected Area Management Board (PAMB) of Mt. Kitanglad, Department of Environment and Natural Resources (DENR) and for conserving and properly managing the threatened, endemic, rare and economically important species of plants and their habitats.

Objectives

The project objectives were to obtain an inventory, and assess and conserve the threatened, endemic, rare and economically important plants in the Mt. Kitanglad Range Natural Park, Bukidnon, Southern Philippines. Specifically, it aimed to (1) identify and describe the vegetation types; (2) determine the diversity of vascular plants; (3) assess their conservation status; (4) record plant habitats and distribution; and, (5) recommend policy measures regarding the protection and conservation of the threatened/endemic species and their habitats.

Methods and materials

Prior Informed Consent (PIC) and selection of local researchers

To satisfy the legal requirements of EO 247 (Bioprospecting) and RA 9147 (Wildlife Resources Conservation and Protection Act), prior informed consent from the community was obtained by presenting the research proposal. Likewise, this research proposal was presented to the members of the Protected Area Management Board (PAMB) of Mt. Kitanglad Range Natural Park for their approval and eventual issuance of the Gratuitous Permit from the Department of Environment and Natural Resources.

Selection of local researchers (Forest Guides) was made with the stakeholders in Sitio Intavas, Barangay La Fortuna, Impasug-ong, Bukidnon based on their sufficient indigenous knowledge of the floral resources in the study sites. Being co-researchers and since the nature of the research is participatory, the Forest Guides were compensated and involved during the entire duration of field work.

Identification and description of vegetation types

Field reconnaissance and a transect survey were conducted to identify and describe the vegetation types by considering the species richness and dominance, canopy cover, tree profile, altitude, location and other ecological parameters. A GPS was used to determine the location of each vegetation type.

Survey, establishment of sampling sites, collection and processing of specimens

Several transects along the landscape were laid out to inventory and assess the plant species observed. Likewise, a transect belt of 2 km x 10 m wide was established per vegetation type. Within the transect belt, an inventory and assessment of plants were conducted, and their local names, uses and altitude were recorded. Representative specimens collected were pressed, poisoned and mounted as herbarium vouchers using the wet method. Duplicates of the herbarium specimens were sent and deposited at the Philippine National Herbarium and Herbarium of the Taiwan Forestry Research Institute.

Diversity Indices

A total of 34 sampling plots, each 20 m × 20 m, were established in all vegetation types, each type with 12 sampling plots except for the upper mossy forest, with 10 plots. Tree enumeration was carried out for all individuals with a diameter at breast height (dbh) of 10 cm and larger. Within these plots, a 5 m × 5 m subplot was laid out to determine the species richness of pteridophytes, of which all occurring individuals were assessed. We assessed species diversity by using the Shannon index of general diversity (H'):

for trees: $H' = - \Sigma\ ndbh/Ndbh \log ndbh/Ndbh$
(where, ndbh = diameter at breast height of individual tree species
Ndbh = total diameter at breast height of all tree species);
and for pteridophytes: $H' = - \Sigma\ [n_i]/N \log [n_i]/N$
(where, n_i = number of individuals in an area,
and N = total number of individuals in an area).

The Species Importance Value (SIV) was computed using the formula of Brower and Zar (1977):

SIV or ni = RD + RF + Rdom
where, RD = relative density, RF = relative frequency, Rdom = relative dominance.

Identification and assessment of conservation status

The collected plants were identified using taxonomic keys from floras and monographs of Merrill (1923-1926); Linder (1987); Madulid (1995); Kalkman et al. (1995-1996); Editorial Committee of the Flora of Taiwan (1996); Rojo (1999); Jebb & Cheek (2001); Cootes (2001); Barcelona et al. (1996); Tan et al. (1996); Zamora & Co (1986); and Amoroso et al. (1993, 1996, 1997).

The assessment of status for each species, whether threatened, endemic, rare or economically important, was determined with the help of the national list of threatened Philippine plants (Fernando et al. 2008), the IUCN (2007) and from published floristic works and monographs.

Definitions of terms adopted from the International Union for the Conservation of Nature (IUCN) (2007), Fernando *et al.* (2008), Zamora (1986) and Department of Environment and Natural Resources (DENR) Administrative Order No. 2007-01 (as defined in its Section 5 of R.A. 9147) include:

a) *Threatened Species* - Actively threatened with extinction and its survival is unlikely without protective measures. Threatened species fall under three categories as defined by Fernando *et al.* (2008):

a1) *Critically Endangered* – A taxon is critically endangered when it is facing an extremely high risk of extinction in the wild in the immediate future.

a2) *Endangered* – A taxon is endangered when it is not critically endangered but is facing a very high risk of extinction in the wild in the medium-term future.

a3) *Vulnerable* – A taxon is vulnerable when it is not critically endangered or endangered but is facing a high risk of extinction in the wild in the medium term future.

a4) *Other threatened species* – A taxon belongs to other threatened species when it is under threat from adverse factors, such as over collection, throughout its range and is likely to move to the vulnerable category in the near future.

a5) *Other wildlife species* – A taxon belongs to other wildlife species when it has been evaluated but does not satisfy the criteria for any of the categories Critically Endangered, Endangered, Vulnerable or Other Threatened Species, but have the tendency to become threatened due to predation and destruction of habitat or other similar causes as may be listed by the Secretary upon the recommendation of the National Wildlife Management Committee.

b) *Rare Species* – Not under immediate threat of extinction but occurring in such small numbers or in such localised or specialised habitat that it could quickly disappear if the environment worsens; needs monitoring.

c) *Depleted Species* – Although sufficiently abundant for survival, the species has been heavily depleted and in decline as a result of natural causes of human activities.

d) *Endemic Species* – Confined to a certain geographical region or its parts.

e) *Economically Important Species* – Based on known usefulness whether medicinal, ornamental, food, construction material, etc.

Results and discussion

Vegetation types and distribution

Transect survey and establishment of sampling plots was carried out along the trail in the northeastern part of Mt. Kitanglad Range Natural Park to identify and describe the vegetation types by considering the coordinates, species richness and dominance, tree profile, altitude, and other ecological parameters (Fig. 1). Three vegetation types were identified from 1200 m asl to the peak of the park as described below (Fig. 2).

The *agro-ecosystem* (08°10'17"N, 124°56'09"E) ranges from 1200 m to 1700 m asl. Potatoes (*Solanum tuberosum* L.), cabbage (*Brassica oleracea* L.), carrots (*Daucus carota* L.) and tomatoes (*Lycopersicum esculentum* Mill.) dominated this vegetation. The original vegetation was dipterocarp forest but this was logged and later converted to agricultural land and planted with cash crops. Threatened plants such as *Cyathea contaminans* (Wall.) Copel., (*anonotong), Podocarpus macrocarpus* de Laub. and *Dicranopteris linearis* (Burm.) Underw. (*agsam*), which is an indicator of a disturbed habitat, was observed at the edge of the vegetable plantation (Fig. 2A). The agroecosystem in Mt. Malindang is also dominated by crops like vegetables, cereals and agroforestry species (Amoroso et al. 2006).

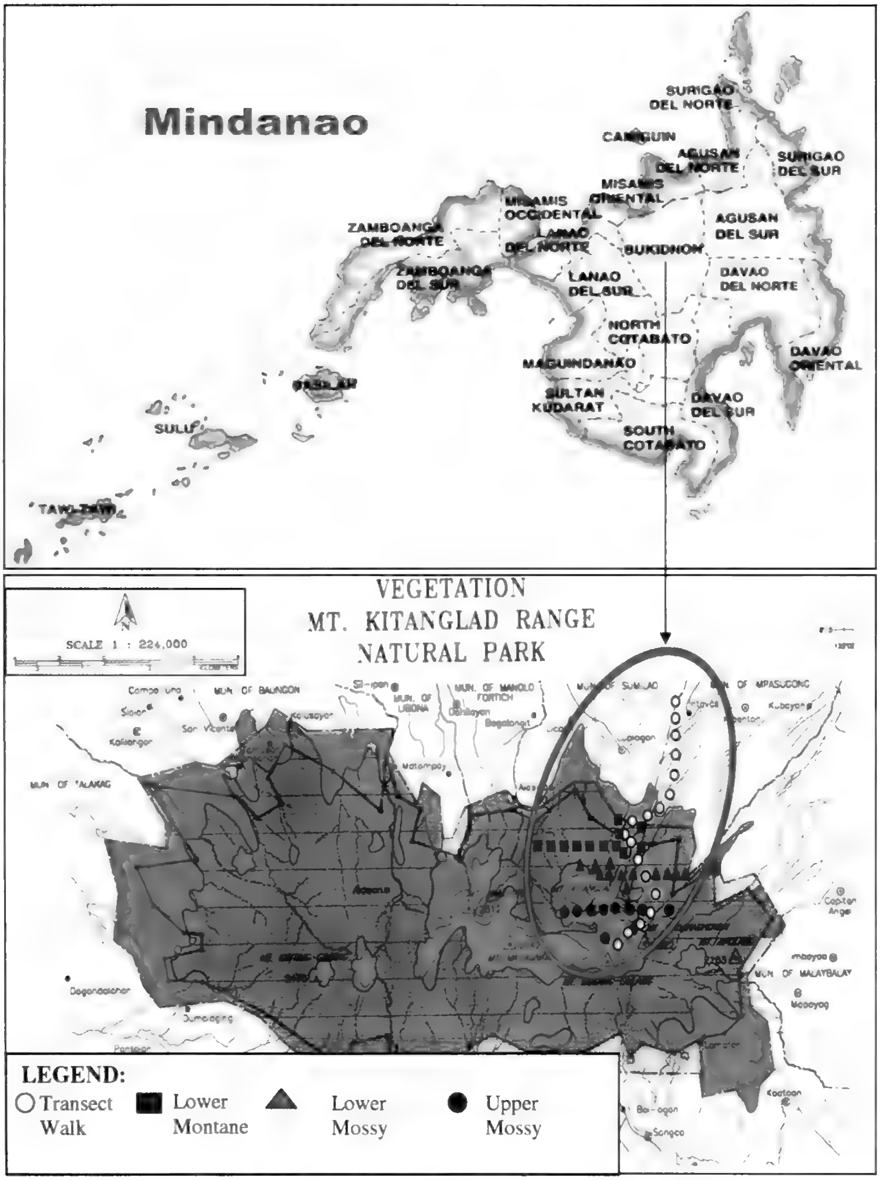

Fig. 1. Location of Bukidnon Province on Mindanao (upper map), and layout of the transect walk and 34 sampling plots in the Mt. Kitanglad Range Natural Park (lower map).

The *lower montane forest* (08°09'54"N, 124°55'58"E) already begins from the foot of Mt. Kitanglad and ranges from 1700 m to 2100 m asl. This forest is characterised by the presence of numerous species of mosses, lichens and other epiphytes. The dominant tree species include *Phyllocladus hypophyllus* Hook.f. (mountain *tungog*), *Lithocarpus spp.* (*ulayan*), *Erythrina subumbrans* (Hasskarl) Merr. (*anii*), while the common shrubs observed included the endemic *Hydrangea scandens* Ser., *Drimys piperata* Hook f. and several *Medinilla* spp. Emergent trees are 5–20 m tall, averaging

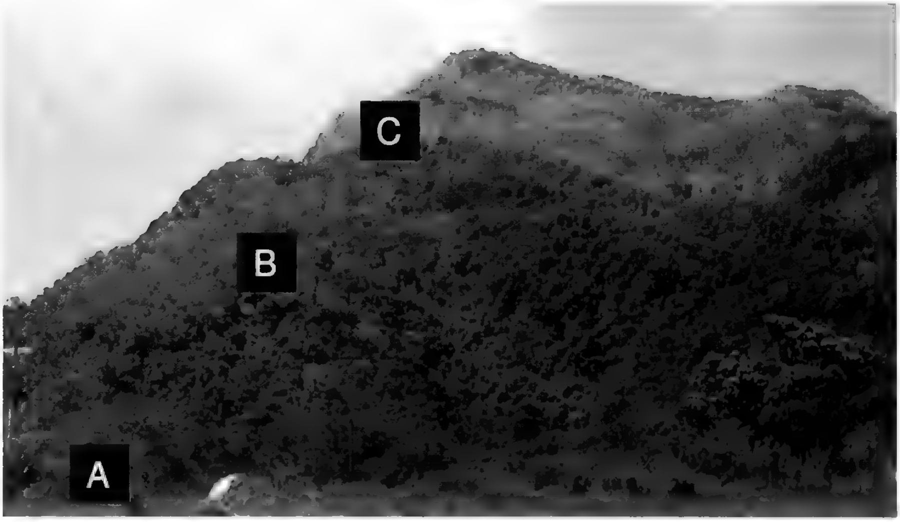

Fig. 2. Panoramic view of Mt. Kitanglad Range Natural Park, Intavas, Impasug-ong, Bukidnon showing the vegetation types. **A.** Agroecosystem. **B.** Montane Forest. **C.** Mossy Forest. Photo by V. Amoroso, June, 2007.

12 m. The moss cover ranges from 50-75%. The edge of the montane forest is usually inhabited by *Trema orientalis* (L.) Blume (*andaluyong*), *Pteridium aquilinum* (L.) Kuhn (*sigpang* or bracken) and *Cyathea* spp. (*Anonotong* or tree ferns) (Fig. 2B). This is similar to what was observed by Amoroso et al. (2006) in the montane forest on Mt. Malindang, which has a high relative humidity and rainfall and has trees on the average taller than in the mossy forest; they also noted that the moss layer was less conspicuous than in the mossy forest.

The *mossy forest* begins from 2100 m asl up to the peak as described below. The branches and trunks of trees and the forest floor were largely covered with mosses, hence the name mossy forest (Amoroso et al. 2006). We consider there to be lower and upper facies of these mossy forests from plant diversity considerations.

(a) The lower mossy forest (08°09'27"N, 124°55'49"E to 08°09'16"N, 124°55'30"E) starts from 2100 m asl, reaching 2400 m asl. Moss cover is thick in this vegetation type, over the ground, roots, trunks and branches of trees. *Lithocarpus* sp., *Phyllocladus hypophyllus* Hook.f. and *Podocarpus* spp. were the most abundant trees. Tree height ranges 7–13 m, with an average of 10 m.

(b) The upper mossy forest (08°09'16"N 124°55'30"E to the peak at 08°08'38"N 124°55'06" E) starts from 2401 m asl to 2900 m asl. Moss cover was very thick in this vegetation type and largely covered the forest floor, roots, and the twisted trunks and branches of trees. *Leptospermum javanicum* Blume was an abundant tree, while *Rhododendron* spp., *Dimorphanthera apoana* (Merr.) Schltr., *Vaccinium* spp. and *Rubus* spp. were abundant shrubs. Tree height ranges 6–12 m, with an average of 9 m.

The summit of the park has an abundance of the dwarf bamboo (*Yushania nitakayamensis* (Hayata) Keng f.) and the wet ground is covered with *Nertera diffusa* (Mutis ex L.f.) Druce, *Sphagnum* moss and lycopods.

Amoroso et al. (2004) observed that the mossy forest of Mt. Malindang was characterised by the presence of small trees with prop roots and aerial roots developing at 1–few meters from the base of irregularly shaped tree trunks. The presence of prop roots appeared to be correlated to steep slopes, which were prevalent in this zone. As in other mossy forests in the Philippines, the trees were dwarfed and their trunks gnarled, especially those that grew near the mountain peak, possibly due to strong wind pressure.

If Mt. Kitanglad has three vegetation types, Mt. Hamiguitan showed five vegetation types (Amoroso et al. 2009), while Mt. Malindang exhibited six (Amoroso et al. 2004).

Species richness and diversity

The sampling plots and transect survey enumerated a total of 661 species, 264 genera, and 106 families of vascular plants (Table 1). There were 439 pteridophyte species, 11 gymnosperm species and 211 angiosperm species.

Table 1. Number of families, genera and species of plants in Mt. Kitanglad Range Natural Park, based on the present study of sampling plots and the transect survey. Of 661 total taxa, 495 were identified to the species level.

Plant group	Number of		
	Families	*Genera*	*Species / Taxa*
Pteridophytes			
Ferns	25	100	408
Lycopods	3	4	31
Gymnosperms	4	8	11
Angiosperms	74	152	211
TOTAL	106	264	661

The Philippines has a total of 9,060 species of vascular plants, or perhaps more (Madulid 1991). Of these, Mt. Kitanglad has 42.8% of the pteridophytes, 33.3% of the gymnosperms and 2.6% of the angiosperms The species richness of vascular plants in Mt. Kitanglad (7.3%) is lower than in Mt. Hamiguitan (9.6%) and Mt. Malindang (12.8%). The lower species richness of angiosperms in Mt. Kitanglad is due to the absence of dipterocarp forest, whereas this forest type was found on Mt. Malindang and Mt. Hamiguitan. Mt. Kitanglad, however, has a higher species richness of pteridophytes compared to the Mt. Hamiguitan and Mt. Malindang (Table 2).

Pteridophyte, as well as tree, diversity decreases from lower montane to mossy forest (Table 3). The same pattern was observed for trees at Mt. Malindang and Mt. Hamiguitan (Amoroso et al. 2006, 2009).

Table 2. Plant species richness of Mt. Kitanglad, Intavas, Bukidnon and two other protected areas in Mindanao, compared with overall statistics for the Philippines.

Plant group	Total number (and percentage) of species				
	Philippines	*Mindanao*	*Malindang* (Amoroso et al., 2006)	*Hamiguitan* (Amoroso et al., 2009)	*Kitanglad*
Pteridophytes	1027	632 (61.5%)	280 (27.3%)	155 (15.0%)	439 (42.8%)
Gymnosperms	33	No data	11(33.3%)	25 (75.8%)	11(33.3%)
Angiosperms	8000+	No data	873 (10.9%)	698 (8.7%)	211 (2.6%)
TOTAL	9060+	No data	1164 (12.8%)	878 (9.6%)	661 (7.3%)

Table 3. Plant species diversity (Shannon index of general diversity, H') in different vegetation types of the Mt. Kitanglad Range. Pteridophyte enumerations are based on 5 m × 5 m plots, with 10 plots in Lower Montane Forest, 12 plots in Lower Mossy Forest, and 10 plots in Upper Mossy Forest. Tree enumerations are based on 20 m × 20 m plots, with 12 plots in Lower Montane Forest and Lower Mossy Forest, and 10 plots in Upper Mossy Forest.

Vegetation type	*Mean number of*				*Mean diversity value*	
	Individuals		*Species*			
	Pteridophytes	Trees	Pteridophytes	Trees	Pteridophytes	Trees
Lower Montane (1700–2100 m)	94.6	26.9	7.48	7.9	0.45	0.80
Lower Mossy (2100–2400 m)	45.8	24.8	9.5	6.9	0.83	0.84
Upper Mossy (2400–2800 m)	48.8	20.2	7.0	4.4	0.69	0.72

The pteridophyte diversity value was higher (H'=0.83) in the lower mossy forest than in both the lower montane and upper mossy forests with H'= 0.45 and 0.69, respectively. Among trees, however, the highest diversity value was obtained in the lower mossy forest (H'=0.84), followed by the lower montane and upper mossy forests with H'=0.80 and H'=0.72, respectively. This implies that the diversity is highest at mid-elevations, although comparison with lowland vegetation types was not possible in this study. As a comparison, mossy forests in Mt. Kitanglad and Mt. Hamiguitan had lower diversity values. However, the upper mossy forest has a significantly reduced diversity compared with the lower mossy forest. In terms of species richness, however, it is clear that there are progressively fewer species from lower montane forest upwards. These facts support the contention of various ecologists that the number of species (i.e., richness) or diversity values at higher altitudes is lower as a response to increasing environmental stresses like wind pressure, steep slopes, thin soil substrates, etc. (Perez 2004).

Species Importance Values (SIV)

Species importance values determine the dominant species in an area and at the same time provide an overall estimate of the influence of these species in the community. The removal of these species from the community will greatly affect the physical and biological structure of the community.

The species of pteridophytes which obtained the highest Species Importance Value (SIV) in the lower montane forest (Table 4) were *Mecodium reinwardtii* (van der Bosch) Copel., *Trichomanes* sp., *Hymenophyllum* sp., *Nephrolepis cordifolia* (Linn.) Presl. and *Grammitis* sp. while for lower mossy forest, they were *Plagiogyria pycnophylla* (Kunze) Mett., *Phymatosorus* sp., *Plagiogyria christii* Copel., *Hymenophyllum* sp. and *Microsorum scolopendria* (Burm.f.). Further, the upper mossy forest species with the highest SIV were *Hymenophyllum* sp., *Asplenium normale* Don, *Dicranopteris*, *Humata repens* (Linn.) Diels, and *Plagiogyria glauca* (Blume) Mett. *Hymenophyllum* sp. and *Plagiogyria christii* were the top two pteridophytes with the highest SIV values on Mt. Kitanglad. This observation is in consonance with the results of Amoroso et al. (2009).

The tree species which obtained the five highest SIV (Species Importance Values) in the lower montane forest includes: *Lithocarpus* sp., *Fagraea blumei* G. Don, *Melicope* sp., *Phyllocladus hypophyllus* and *Cinnamomum mercadoi* Vidal. The lower mossy forest had the following species with the five highest SIV: *Lithocarpus* sp., *Phyllocladus hypophyllus*, *Leptospermum* sp., *Syzygium* sp. and *Podocarpus costalis* C. Presl. For the upper mossy vegetation, *Leptospermum* sp., *Dacrycarpus cumingii* (Parl.) de Laub., *Fagraea blumei*, *Phyllocladus*, and *Podocarpus* sp. were the five species with the highest SIV. For the trees, *Leptospermum* sp. and *Lithocarpus* sp. had the highest SIV value on Mt. Kitanglad. This finding is also supported by the study of Amoroso et al. (2009). *Lithocarpus* sp. ranked first in both lower montane and lower mossy forests of Mt. Kitanglad, with SIV of 115% and 94.32%, respectively. At Mt. Hamiguitan, *Agathis philippinensis* Warb. ranked first in both lower montane and mossy forest. It is noteworthy to mention that *Hymenophyllum* sp. and *Plagiogyria christii* with high SIV were observed in the three vegetation types (Amoroso et al. 2009).

According to Krebs (1994), variation in important species may be caused by differences in the response of various species to environmental conditions. He also noted that elevation provides complex environmental gradients including temperature, rainfall and relative humidity. It was noted that the species composition of the three vegetation types here differed, suggesting that habitat differences catered differently to the requirements of tree species.

Table 4. Species importance values of pteridophytes and trees in the different vegetation types.

Vegetation	Pteridophytes	SIV (%)	Trees	SIV (%)
Lower Montane (1700–2100 m)	*Mecodium reinwardtii*	94.75	*Lithocarpus* sp.	115.0
	Trichomanes sp.	80.67	*Fagraea blumei*	85.67
	Hymenophyllum sp.	76.63	*Melicope* sp.	76.42
	Nephrolepis cordifolia	72.27	*Phyllocladus hypophyllus*	66.95
	Grammitis sp.	64.32	*Cinnamomum mercadoi*	64.84
Lower Mossy (2100–2400 m)	*Plagiogyria pycnophylla*	154.67	*Lithocarpus* sp.	94.32
	Phymatosorus sp.	137.00	*Phyllocladus hypophyllus*	83.50
	Plagiogyria christii	102.01	*Leptospermum* sp.	80.32
	Hymenophyllum sp.	85.96	*Syzygium* sp.	70.16
	Microsorum scolopendria	81.99	*Podocarpus costalis*	60.00
Upper Mossy (2400–2800 m)	*Hymenophyllum* sp.	209.66	*Leptospermum* sp.	168.91
	Asplenium normale	138.94	*Dacrycarpus cumingii*	78.99
	Dicranopteris linearis	111.93	*Fagraea blumei*	72.91
	Humata repens	97.46	*Phyllocladus hypophyllus*	57.29
	Plagiogyria glauca	95.11	*Podocarpus costalis*	56.87

Tree profile

Table 5 shows the mean number of species and individuals, average height and average diameter at breast height (dbh) of trees in the sampled plots of the different vegetation types. The lower montane forest obtained the highest average number of individuals in 20 m × 20 m plots with 26.9 individuals, while upper mossy forests had the lowest average number of trees with 20.2 individuals. As altitude increases, the average number of individuals (of 10 cm diameter or bigger) decreases. The highest average height (11.12 m) and average dbh (39.30 cm) were recorded from trees of the lower montane forest. These values decrease with elevation. The lowest value for average height and average dbh were recorded in the upper mossy forest. *Lithocarpus* sp. was the tallest tree recorded in the lower montane forest and lower mossy forest, attaining 25.0 m and 24 m, respectively. *Dacrycarpus cumingii* (20 m) were tallest in the upper mossy forest.

Tree profile diagrams for the 34 plots were individually made to record the species distribution and indicate relative heights of trees in the 20 m × 20 m plots. From these, canopy cover in the sampling plots were calculated and ranged from 70–95% in the lower montane forest compared 60–80% in the lower mossy forest, and

Table 5. Mean number of individuals, average height and diameter at breast height (dbh) of trees in different vegetation types on Mt. Kitanglad Range, Intavas, Bukidnon.
Calculated based on enumerations of 12 plots each in Lower Montane Forest and Lower Mossy Forest, and 10 plots in Upper Mossy Forest; each plot 20 m × 20 m.

Vegetation type	Mean number of		Average height (m)	Average dbh (cm)
	Individuals	*Species*		
Lower Montane (1700–2100 m)	26.9	7.9	11.12	39.30
Lower Mossy (2100–2400 m)	24.8	6.9	9.60	21.69
Upper Mossy (2400–2800 m)	20.2	4.4	7.03	16.60

10–15% in the upper mossy forest. Since tree coordinates were taken in each of the 34 sampling plots, long-term monitoring of tree dynamics will be possible.

Assessment of conservation status

The habitat of the plants, whether epiphytic, terrestrial or petrophytic lithophytic, was noted. The distribution of threatened, endemic and economically important species of plants was mapped based on elevation and vegetation types. Recording of altitudinal distribution of the threatened, endemic, and economically important species in these vegetation types will be an important basis in allocating priority to their protection and conservation.

The conservation status of each species was noted and recorded. This was carried out to establish a foundation for their protection, conservation and monitoring. Of the total number of taxa, only 495 species have been identified up to the species level. Of these species, about 92 species were recorded as threatened, 82 rare species, 108 endemic species, 50 economically important species, 56 species as new records for the locality and 20 species as new records for the Philippines (Table 6).

Out of the 9060+ vascular plant species of the Philippines, 530 are threatened, including 85 pteridophytes, 5 gymnosperms and 440 angiosperms (Fernando et al. 2008). Of this number, 17.4% threatened species are located in Mt. Kitanglad comprising 77, 7 and 8 species of pteridophytes, gymnosperms, and angiosperms, respectively (Table 7). The percentage of threatened species in Mt. Kitanglad is 7% and 11% higher than in Mt. Malindang and Mt. Hamiguitan, respectively.

The Philippines has a total of 3557 endemic species, including 351 pteridophytes, 6 gymnosperms, and 3200 angiosperms (Madulid 1991, Fernando et al. 2008). Mt. Kitanglad has 21% of this endemism, which is higher than for Mt. Malindang, but lower than for Hamiguitan. It has, however, a higher percentage endemism of pteridophytes as compared to both mountain ranges (Table 8). The high species endemism in Mt. Hamiguitan may be due to effects of the specialised ultramafic geology there.

Table 6. Number of threatened, endemic and economically important plants, and new records for Mt. Kitanglad Range Natural Park, Intavas, Impasug-ong, Bukidnon. TS - Threatened species; RS - Rare species; ECS - Endemic species; NRL - New record for locality; EIS - Economically important species; NRP - New records for the Philippines.

Plant groups	*Status*					
	TS	RS	ECS	EIS	NRL	NRP
Pteridophytes						
Ferns	75	70	43	40	47	19
Lycopods	2	4	2	3	3	1
Gymnosperms	7	4	1	3	0	0
Angiosperms	8	4	62	4	6	0
TOTAL	*92*	*82*	*108*	*50*	*56*	*20*

Table 7. List of some threatened and endemic species in Mt. Kitanglad Range Natural Park. Conservation status rankings: CR - Critically Endangered; EN - Endangered; OTS - Other Threatened Species; OWS - Other Wild Species; VU - Vulnerable; ECS - Endemic. Vegetation types: LMo - Lower Montane; LM - Lower Mossy; UM - Upper Mossy. A denotes the agro-ecosystem lower down.

	Family	Species	Status	Vegetation type	Altitude (m)
1	Aspleniaceae	*Asplenium nidus* L.	VU	A	1711
2	Aspleniaceae	*Asplenium vittiforme* Cav.	VU	LMo	1935, 2030
3	Blechnaceae	*Blechnum fraseri* (A. Cunningham) Luerss.	VU	LM, UM	2280–2530
4	Cyatheaceae	*Cyathea elmeri* Copel.	VU	LMo	1935–2050
5	Cyatheaceae	*Cyathea philippinensis* Baker	VU, ECS	LMo	2030
6	Cyatheaceae	*Cyathea contaminans* (Wall.) Copel.	VU	LMo	2030
7	Dennstaedtiaceae	*Dennstaedtia williamsi* Copel.	EN	LMo	2020
8	Dryopteridaceae	*Polystichum elmeri* Copel.	OWS	LM	2280
9	Ophioglossaceae	*Botrychium daucifolium* Wall.	VU	LM	2300
10	Polypodiaceae	*Aglaomorpha cornucopia* (Copel.) Roos	VU, ECS	Mo	1797
11	Polypodiaceae	*Aglaomorpha heraclea* (Kuntze) Copel.	VU	LM	2245

12	Polypodiaceae	*Microsorum punctatum* (L.) Copel.	VU	LMo	1711
13	Polypodiaceae	*Microsorum sarawakense* (Baker) Ching	VU	LMo	1797
14	Polypodiaceae	*Microsorum scolopendria* (Burm.f.)	VU	LMo, LM	1797–2280
15	Psilotaceae	*Tmesipteris lanceolata* Dang.	VU	LMo, LM, UM	2050–2600
16	Araucariaceae	*Agathis philippinensis* Warb.	VU	LMo	1945
17	Podocarpaceae	*Podocarpus costalis* C. Presl.	VU	LMo	2113
18	Podocarpaceae	*Podocarpus macrocarpus* de Laub.	OWS	LMo, LM, UM	1985–2840
19	Ericaceae	*Rhododendron kochii* Stein	EN, ECS	LMo, LM	2245–2495
20	Ericaceae	*Rhododendron javanicum* (Blume)	EN	LMo, LM	2245–2495
21	Lauraceae	*Cinnamomum mercadoi* Vidal	VU, ECS	LMo, LM	2050–2300
22	Rosaceae	*Rubus heterosepalus* Merr.	OTS, ECS	LMo	2010

Table 8. Endemism in the Philippines compared to that at Mt. Kitanglad Range, Intavas, Bukidnon. Based on specimens identified to the species level. A dash refers to lack of data. Malindang data from Amoroso et al. (2006); Hamiguitan data from Amoroso et al. (2009).

	Total number of species (Tspp) and number endemic (*Espp*)									
Plant group	*Philippines*		*Mindanao*		*Malindang*		*Hamiguitan*		*Kitanglad*	
	Tspp	*Espp*	Tspp	*Espp*	Tspp	*Espp*	Tspp	*Espp*	Tspp	*Espp*
Pteridophytes	1027	351	632	183	246	28 *(11%)*	99	9 *(9%)*	363	45 *(12%)*
Gymnosperms	33	6	—	3	11	3 *(27%)*	13	1 *(7%)*	11	1 *(9%)*
Angiosperms	8000+	3200	—	—	450	107 *(23%)*	365	153 *(41%)*	121	62 *(51%)*
TOTAL	9060+	3557	—	—	825	138 *(16%)*	477	163 *(34%)*	495	108 *(21%)*

New records

Nineteen species of fern and one species of fern ally are new records for the Philippines, while 50 species of pteridophyte and six species of angiosperm are new records for the locality (Table 6). A significant output of this research was the new record of *Athyrium erythropodum* Hayata (Woodsiaceae) (Fig. 3) for the Philippine flora (Liu et al. 2008). This species had previously been recorded as endemic to Taiwan and was only subsequently discovered on Mt. Kitanglad. Another species newly recorded for the Philippines is *Huperzia monticola* Underw. & F.E Loyd (Fig. 4). This was earlier reported in Sumatra, Indonesia, and is now recorded for the first time on Mt. Kitanglad.

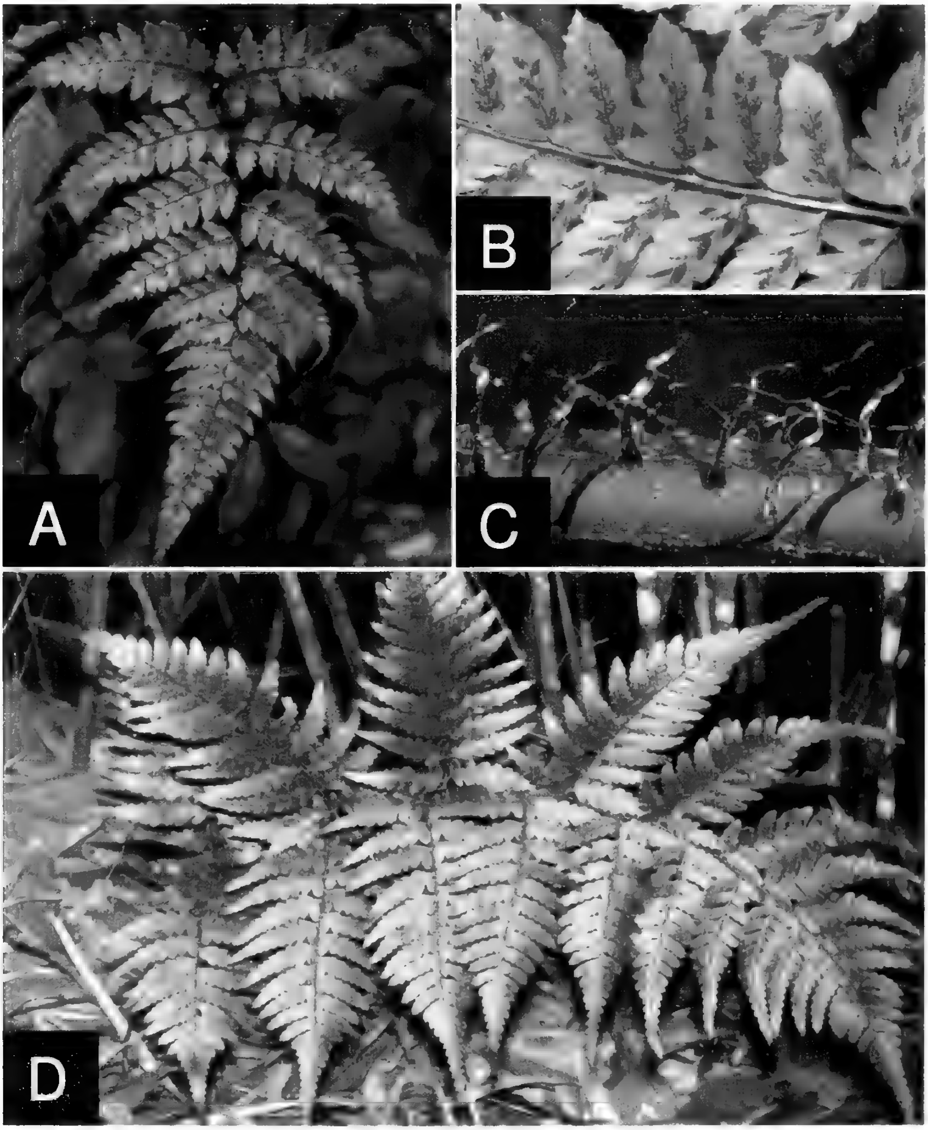

Fig. 3. *Athyrium erythropodum* Hayata, a new Philippine record. **A.** Frond. **B.** Sori with indusia. **C.** Scales on stipe base. **D.** habit. Photographs from Yea-Chen Liu et al. 2009.

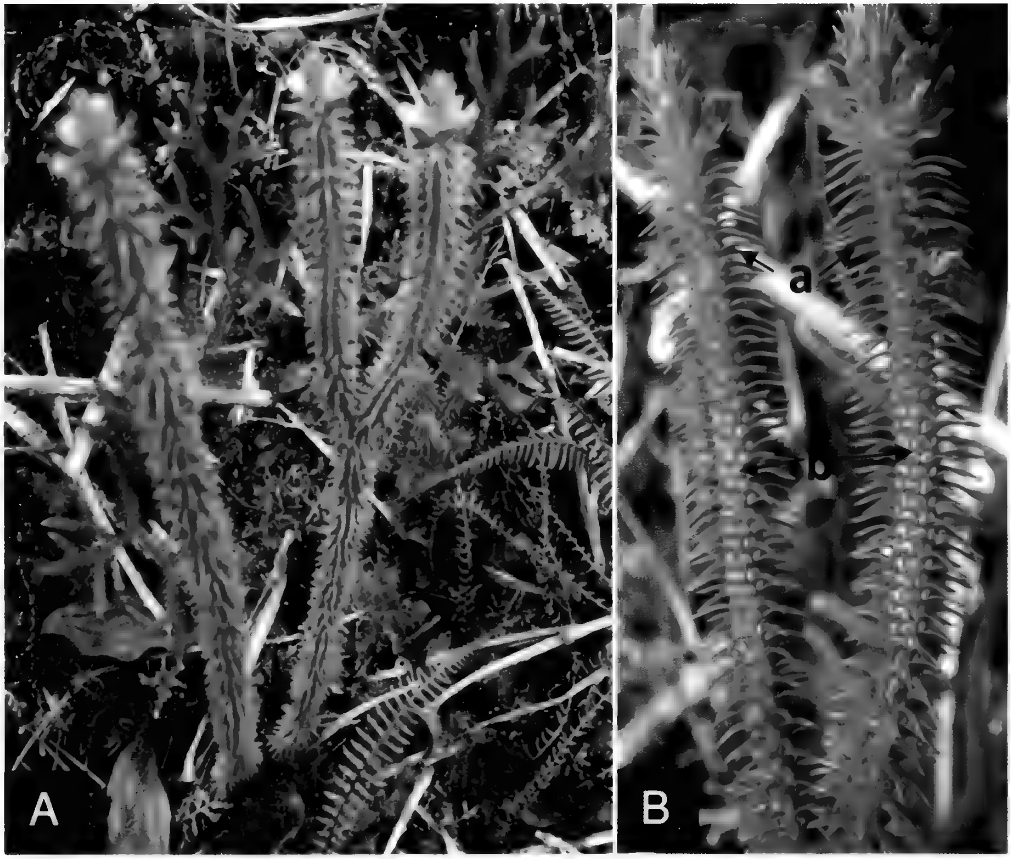

Fig. 4. *Huperzia monticola* Underw. & F.E. Loyd. **A.** Habit. **B.** Aerial axis showing microphylls (a) and sporangia (b). Photos by V. Amoroso.

Dissemination of Information, Education and Communication (IEC) Materials
The Information, Education and Communication (IEC) materials were prepared in the form of flyers, with relevant information such as scientific name, local name, family name and status of the floral species (Fig. 5). These help to enhance community awareness for the conservation and protection of these species, and will be disseminated to the community and local researchers and guides for their use.

Policy recommendations

The results of this project should be useful to Local Government Units (LGUs) of Impasug-ong and other municipalities and communities around the park; the Protected Area Wildlife Division (PAWD) of the Department of Environment and Natural Resources; and the Protected Area Management Board (PAMB) in the formulation of policies and ordinances to protect and conserve the remaining botanical resources of the Mt. Kitanglad Range Natural Park.

Asplenium nidus
ASPLENIACEAE

Asplenium vittaeforme
ASPLENIACEAE

Blechnum fraserii
BLECHNACEAE

Botrychium daucifolium
OPHIOGLOSSACEAE

Ophioglossum pendulum
OPHIOGLOSSACEAE

Aglaomorpha cornucopia
POLYPODIACEAE

Agathis philippinensis
ARAUCARIACEAE

Podocarpus costalis
PODOCARPACEAE

Podocarpus macrocarpus
PODOCARPACEAE

Rhododendron kochii
ERICACEAE

Rhododendron javanicum
ERICACEAE

Cinnamomum mercadoi
LAURACEAE

Fig. 5. Some threatened plants of Mt. Kitanglad, Bukidnon, Mindanao. Photos by V. Amoroso.

Recommended policies for the PAMB include: (1) The LGU's of Intavas and other LGUs around the park should officially organise their porters/guides for long-term monitoring of threatened and endemic species. (2) *Ex-situ* and *in-situ* conservation of species and habitats should be carried out to protect the remaining endemic, threatened, rare, and economically important species of plants. For *ex-*

situ conservation, each municipality should have an economic garden / nursery to propagate their threatened, endemic and economically important plants. (3) Collection of threatened and endemic species should be regulated. (4) Denuded mountains should be planted with indigenous tree species. (5) Threatened and endemic species found in agricultural areas should be protected. (6) Mountaineers / hikers should be given proper orientation before trekking and should follow forest guides in their trekking. Temporary campsites at the middle zone (about 2000 m asl) should be discouraged because of the presence of threatened vascular plants.

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Phylogenetic study of the *Hottarum* Group (Araceae: Schismatoglottideae) utilising the nuclear ITS region

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ABSTRACT. Recent phylogenetic analyses of the tribe Schismatoglottideae (Araceae) elucidated a well-supported but internally unresolved crown group comprising *Schismatoglottis sarikeensis* (Bogner & M.Hotta) A.Hay & Bogner, previously placed in the genus *Hottarum* Bogner & Nicolson, the genus *Phymatarum* M.Hotta, and a number of species either novel or hitherto placed in *Schismatoglottis* Zoll. & Moritzi. The clade is particularly interesting in that it is centred in northern central Sarawak (Malaysian Borneo), north of the Lupar Divide and appears to represent an autochthonous radiation point for evolutionary activity isolated from the major tribal radiations in south-western Sarawak. Former *Hottarum* species (with the exclusion of *H. truncatum*) transferred to *Piptospatha* and *Schismatoglottis* are misplaced. All except *Bakoa lucens* (Bogner) P.C.Boyce & S.Y.Wong belong to this supra-Lupar Divide grouping. This study was undertaken to test the validity and phylogeny of the genus *Hottarum* utilising the nuclear ITS region.

Keywords. *Hottarum*, ITS region, Lupar Divide, phylogeny, *Phymatarum*, *Schismatoglottis*

Introduction

The genus *Hottarum* Bogner & Nicolson previously comprised of four rheophytic species, all endemic to Borneo (Mayo et al. 1997). These include the type species, *Hottarum truncatum* (Bogner 1978), from Sg. (river) Kakus, Tatau, Bintulu, Sarawak, and a further three species: *H. lucens* (Bogner 1983), *H. sarikeense* (Bogner & Hotta 1983) and *H. kinabaluense* (Bogner 1984). *Hottarum brevipedunculatum* (Okada & Mori 2000) was subsequently described.

In dismantling *Hottarum*, Bogner & Hay (2000) placed the constituent taxa of *Hottarum* (i.e., including the type) into *Piptospatha*, and *H. sarikeense* was placed into *Schismatoglottis*, based purely on morphological characters. *Piptospatha sensu* Bogner & Hay (2000) differs from *Schismatoglottis* by its unconstricted spathe and in having seeds with an extended micropylar appendage. *Piptospatha sensu* Wong & Boyce (2010b) is further defined from *Schismatoglottis* by the peduncle erect at fruit dispersal, with the persistent lower fruiting spathe forming a funnel-form splash cup, and pistils connate into a syncarpium (or rarely free but coherent).

Phylogenetic analyses of the tribe Schismatoglottideae (Wong et al. 2010), with a well-supported molecular profile and compelling morphological peculiarities, supported the removal of *H. lucens* to a new genus, *Bakoa* (= *Bakoa lucens*; Wong & Boyce 2010a) and *H. kinabaluense* to the generically novel *Ooia* (= *Ooia kinabaluensis*; Wong & Boyce 2010b). Recently, another former *Hottarum* species, *H. brevipedunculatum* was shown to represent a second species of *Bakoa* (*B. brevipedunculata*; Wong 2011). These transfers leave a core of species, including the nomenclatural type (*Hottarum truncatum*), *Hottarum sarikeense*, *Schismatoglottis josefii* A.Hay, and three undescribed species in a *Phymatarum* + *Hottarum* clade.

Materials and methods

Sampling

Twenty taxa were selected. Nine taxa formed the ingroup, including the type of *Hottarum*, *H. truncatum*; *H. sarikeense* (two accessions), *Schismatoglottis josefii*, and its putative sister taxa, *Phymatarum borneense* (two accessions), and three unplaced taxa (*Schismatoglottis* sp. A [AR-114], *S.* sp. B [AR-135] and *S. 'petradoxa'* [AR-920]). Eleven outgroup taxa were selected based on the results from Wong et al. (2010), and comprise *Schismatoglottis* (2 species), *Aridarum* (7 species) and *Bucephalandra* (2 accessions). Appendix A lists all the taxa and its respective localities, together with voucher information and GenBank accession numbers. Vouchers are deposited with the Herbarium of the Sarawak Forestry Department (SAR).

DNA extraction, PCR and sequencing

Total DNA was extracted using a modified version of the 2X CTAB protocol (Doyle & Doyle 1987) with the addition of PVP (PolyVinylPyrrolidone) as described by Gauthier et al. (2008). ITS1 (Internal Transcribed Spacer 1) and ITS 2 were amplified using the primer pairs 1F/1R and 3F/4R, respectively (White et al. 1990). Polymerase chain reactions (PCRs) were conducted in a total reaction volume of 20 μl comprising 1X buffer, 0.1mM dNTP mix, 0.2mM of each primer, 2.0mM $MgCl_2$, 2 units Taq DNA polymerase and 2 μl of DNA extract). 1 μl of DMSO was added to each reaction for improved amplification.

PCR conditions included an initial 2-min denaturation at 95°C, 40 cycles of 1-min at 95°C (denaturation), 1-min at 50°C-60°C (annealing), and 2-min at 72°C (extension), followed by a final 10-min extension at 72°C. PCR products were visualised on 1.5% or 2.0% agarose gels. Desired products were purified and sent for sequencing.

Sequence alignment and phylogenetic analyses

All sequences obtained were manually checked, edited, assembled and aligned using the BioEdit version 7.0.5 (Hall 1999). Gaps were treated as insertions or deletions of nucleotides (indels).

Maximum parsimony (MP) analyses were performed using PAUP* v.4.0b10 (Swofford 2002) according to the parameters described by Wong et al. (2010), except that 100,000 trees were saved at the second round of tree bisection-reconnection (TBR) branch swapping. Tree topologies were interpreted with bootstrap values generated from RAxML (Randomized Axelerated Maximum Likelihood: Stamatakis et al. 2008) for 100 replicates and repeated 10 times to generate 1000 replicates. Bootstrap support values were taken as weak (50–74%), moderate (75–84%) or strong (85–100%) as applied by Richardson et al. (2000).

Results and discussion

Analysis of the ITS region

Total aligned nucleotides for the ITS region for 20 taxa comprise 879 bp. The sequence length varies from 770 bp (*Aridarum crassum*, AR-1605) to 803 bp (*Phymatarum borneense*, AR-1931). A large deletion of indels (46 bp) was found in the type, *Hottarum truncatum* (AR-3080) at the position 159 to 204. Indels were found less beyond the position 500 bp for all 20 taxa. The ITS region was rich with the GC nucleotide. All characters are of the type 'unord' and have equal weight. 771 characters from the entire sequences are constant and 58 variables characters (6.6%) are parsimony-uninformative. The remaining 50 characters (5.7%) were parsimony-informative, resulting in 29 most parsimonious trees with a tree length of 136 steps, consistency index (CI) of 0.85 and a retention index (RI) of 0.82. These trees also generated a rescaled consistency index (RC) of 0.69 and homoplasy index (HI) of 0.15. CI and HI with the exclusion of uninformative characters were 0.72 and 0.28, respectively.

The tree topology of the maximum parsimony (MP) 50% majority rule (not shown) differed in the *Bucephalandra* – *Hottarum truncatum* (AR-3080) and the *Aridarum* clades formed, as compared with the maximum likelihood (ML) tree (Fig. 1) from RAxML. The bootstrap values (BS) for the MP tree were generated and stopped at 411 replicates due to computing limitations. Both MP and ML trees strongly support the previous phylogenetic study by Wong et al. (2010). *Schismatoglottis josefii* together with *H. sarikeense* formed a monophyletic clade (Clade A in Fig. 1) with parsimony bootstrap value, BS_{PA} and likelihood bootstrap value, BS_{ML} of 100%. Clade A is weakly associated with Clade B (37% BS_{ML}). Clade B itself is well supported (85%) and comprises the three unplaced taxa (*Schismatoglottis* sp. A, *Schismatoglottis* sp. B and *Schismatoglottis* '*petradoxa*'). The *Schismatoglottis* sp. B groups with *Schismatoglottis* '*petradoxa*' with weak BS_{PA} and BS_{ML} of 60% and 72%, respectively. *Phymatarum borneense* (Clade D) is recovered as a monophyletic genus (BS_{PA} BS_{ML}=100%). This genus is sister to the rest of the taxa including clusters containing *Hottarum truncatum* (type species of *Hottarum*) – *Aridarum* (Clade C). *Hottarum truncatum* (AR-3080) received low likelihood bootstrap support for its association with the *Aridarum* species (BS_{ML}=55%) in Clade C. As this is considered insignificant, the *Hottarum truncatum* – *Aridarum* clusters are taken as remaining unresolved.

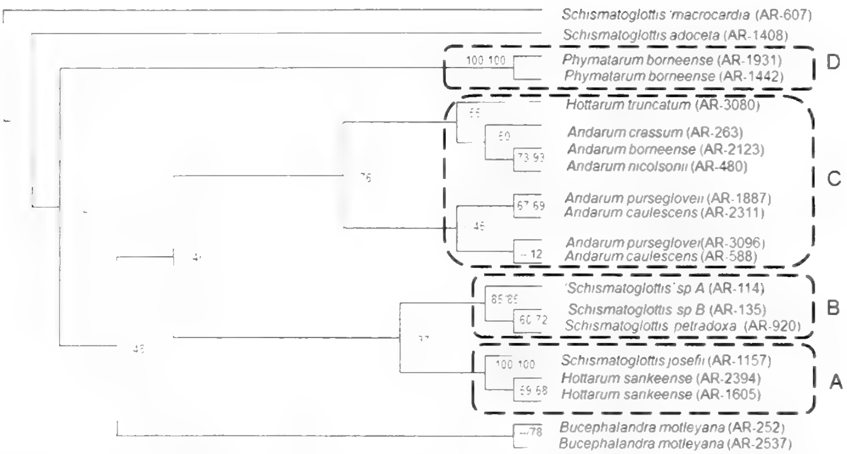

Fig. 1. The maximum likelihood tree obtained from RAxML with ITS sequences. Numbers next to branches are values for BS_{PA}/BS_{ML}. BS_{PA} = bootstrap value for maximum parsimony. BS_{ML} = bootstrap value for maximum likelihood.

Conclusion

Hottarum truncatum (=*Piptospatha truncata*, the type species for *Hottarum*), is shown to be separated from *H. sarikeense* in this study. The rest of the species formerly placed in *Hottarum* have been shown to be misplaced as well. The former *Hottarum* species: *H. lucens* (= *Piptospatha lucens*) and *H. brevipedunculatum* (= *Piptospatha brevipedunculata*) were transferred to a new genus, *Bakoa* P.C.Boyce & S.Y.Wong (Boyce & Wong 2008, Wong 2011) and *Hottarum kinabaluense* (= *P. kinabaluensis*) was transferred to a novel genus, *Ooia* (Wong & Boyce 2010b).

Although *H. truncatum* is sister to *Aridarum*, the weak likelihood bootstrap values do not support the placement of *Hottarum truncatum* within *Aridarum*. A group comprising *Schismatoglottis josefii* and *H. sarikeense*, and another group of 3 novel species from central Sarawak, are well supported clades (with 100% and 85% support, respectively). However, their generic assignment awaits the results of analyses with additional gene regions.

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Appendix A. Taxa included in the study: GenBank accession numbers for sequences used, voucher specimen numbers and collection localities. *'Schismatoglottis'* = unplaced and undescribed taxa; *'macrocardia'* and *'petradoxa'* = nomenclatural taxa yet to be described; taxa are arranged alphabetically following the taxonomic position of Mayo et al. (1997), Bogner & Hay (2000), Hay & Yuzammi (2000) and Wong et al. (2010).

Species	GenBank accession no.	Voucher number	Collection locality / coordinates
Aridarum borneense	JN544438	AR-2123	Sungai Bungen, Kubah National Park, Matang, Kuching, Sarawak, 01°36′30.9″N 110°11′35.0″E
Aridarum caulescens	JN544440	AR-2311	Melinau Gorge, Mulu National Park, Nanga Medamit, Limbang, Sarawak, GPS position not available.
Aridarum caulescens	JN544428	AR-588	Bukit Satiam, Bintulu, Sarawak, 02°58′47.6″N 112°56′37.5″E
Aridarum crassum	JN544426	AR-263	Gunung Gaharu, Pantu, Sri Aman, Sarawak, 01°01′19.5″N 110°52′52.8″E
Aridarum nicolsonii	JN544427	AR-480	Trail above Camp Permai, Santubong, Kuching, Sarawak, 01°45′49.0″N 110°19′07.4″E
Aridarum purseglovei	JN544435	AR-1887	Bukit Satiam, Bintulu, Sarawak, 02°59′13.3″N 112°55′57.5″E
Aridarum purseglovei	JN544444	AR-3096	Sg. Likau, GT Plantations, Tatau, Bintulu, Sarawak, 02° 43′53.6″N 113°25′19.1″E
Bucephalandra motleyana	JN544425	AR-252	Gunung Gaharu, Pantu, Sri Aman, Sarawak, 01°02′39.5″N 110°53′18.3″E
Bucephalandra motleyana	JN544442	AR-2537	Bukit Kelam, Sintang, Kalimantan Barat, Indonesia, 00°05′30.1″N 111°39′03.3″E
Hottarum sarikeense	JN177489	AR-2394	Sg. Pedali, Lubok Antu, Sri Aman, Sarawak, 01°11′58.9″N 112°03′27.0″E
Hottarum sarikeense	JN544434	AR-1605	Sg. Lepong, Sarikei, Sarawak, 01°57′12.9″N 111°30′34.9″E
Hottarum truncatum	JN544443	AR-3080	Sg. Pandan Kecil, Trail behind Camp C, GT Plantations, Tatau, Bintulu, Sarawak, 02°42′40.1″N 113°20′37.9″E

Phymatarum borneense	JN544433	AR-1442	Belaga Road, Sebauh, Bintulu, Sarawak, 03°03′34.3″N 113°42′16.4″E
Phymatarum borneense	JN544436	AR-1931	Trail to Deer Cave, Mulu National Park, Mulu, Miri, Sarawak, 04°02′23.8″N 114°48′54.6″E
Schismatoglottis adoceta	JN544432	AR-1408	Road junction, km 10 Bakun- Bintulu-Miri, Kapit, Sarawak, 02°50′51.7″N 114°01′57.6″E
Schismatoglottis josefii	JN544431	AR-1157	Sg. Pedali, Nanga Sumpa, Batang Ai, Lubok Antu, Sri Aman, Sarawak, 01°11′58.9″N 112°03′27.0″E
Schismatoglottis 'macrocardia'	JN544429	AR-607	Bukit Satiam, Bintulu, Sarawak, 02°59′26.1″N 112°55′54.4″E
Schismatoglottis 'petradoxa'	JN544430	AR-920	Km 65 road to Camp Gahada, Rejang Wood Concession, Nanga Gaat, Kapit, Sarawak, 01°41′59.7″N 113°31′13.7″E
'Schimatoglottis' sp. A	JN544423	AR-114	Sg. Piat, Nanga Gaat, Kapit, Sarawak, 01°38′09.1″N 113°24′09.9″E
'Schismatoglottis' sp. B	JN544424	AR-135	Stream below Camp Gahada, Nanga Gaat, Kapit, Sarawak, 01°41′49.4″N 113°26′16.3″E

Dendrobium (Orchidaceae): To split or not to split?

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ABSTRACT. *Dendrobium* Sw. is one of the three largest orchid genera, with around 1580 species if certain currently accepted satellite genera are included. Until recently, no serious attempts have been made to split up this important genus into smaller genera. An infrageneric classification at the sectional level, largely due to Schlechter, has been accepted by most workers. Recent analyses based on DNA markers by Yukawa, Clements, and others have provided new insights into the phylogeny of *Dendrobium*. Their work shows that *Dendrobium* is not monophyletic when the satellite genera are excluded. This led to proposals to split up *Dendrobium* into as many as fifty genera, largely along the lines of Schlechter's sections. However, the data do not suggest any single, evident way to do the splitting. Here it is argued that a broad concept of the genus *Dendrobium*, which includes genera like *Cadetia* Gaudich., *Flickingeria* A.D.Hawkes and *Epigeneium* Gagnep., among others, is to be preferred. The comparable cases of other large orchid genera are briefly discussed and some observations are made on character evolution in *Dendrobium* and the origin of the genus in light of DNA-based phylogenies.

Keywords. Classification, *Dendrobium*, generic concepts, molecular phylogeny, Orchidaceae

Introduction

In its traditional, broad delimitation, *Dendrobium* Sw. is one of the three largest orchid genera (Cribb & Govaerts 2005: 1197 spp.) as well as one of the most important in commercial horticulture. Certain species of this genus are in high demand in traditional Chinese medicine, which puts wild populations of these species under pressure from (illegal) collecting in China and neighbouring countries. Habitat destruction threatens the survival of many more species throughout the range of the genus. The taxonomy of *Dendrobium* is therefore of interest not only to botanists, but also to orchid growers, ecologists and conservationists.

Dendrobium belongs to subtribe Dendrobiinae in the tribe Dendrobieae of the subfamily Epidendroideae, the largest of the five subfamilies within the Orchidaceae. Most species of *Dendrobium* are epiphytes in primary forest, less often lithophytes; only very few are obligate terrestrials. The range of the genus extends from Sri Lanka and India throughout tropical Asia, north to Japan, east to Tahiti, and south to New Zealand.

Prior to the advent of molecular methods, various classifications had been proposed for *Dendrobium* and related genera, as summarised in Wood (2006). Dressler

(1981, 1993) expressed a consensus view when he listed six genera as constituting the subtribe Dendrobiinae: *Cadetia* Gaudich., *Dendrobium*, *Diplocaulobium* (Rchb.f.) Kraenzl., *Epigeneium* Gagnep., *Flickingeria* A.D.Hawkes (*Ephemerantha* P.F.Hunt & Summerh.), and *Pseuderia* Schltr. In this view, the Dendrobiinae consist of the very large and complex genus *Dendrobium* next to a number of much smaller, more homogenous genera, which had all been treated as sections of *Dendrobium* in the past. Rudolf Schlechter (1911–1914) must be credited with presenting an infrageneric classification of *Dendrobium* that has been adopted with few modifications by most subsequent workers. This, however, applies only to the section level. Schlechter's system of subgenera is almost entirely artificial, being based on the application of single defining character states, such as the presence or absence of a sheathing leaf base. As we now know, this does not lead to phylogenetically meaningful groupings in this subtribe.

The pioneering studies by Yukawa and co-workers (1993, 1996, 2000, 2001) using DNA markers (matK and ITS) have provided a number of insights, which were confirmed and extended by later studies (Clements 2003, 2006; Wongsawad et al. 2005; Burke et al. 2008; Sathapattayanon 2008):

1. Dendrobiinae consists of three main clades:
    I. A predominantly continental Asian and West Malesian clade that includes the type species of *Dendrobium* (*D. moniliforme* (L.) Sw.).
    II. A predominantly East Malesian - Australian - New Caledonian clade that includes, e.g., *D. bigibbum* Lindl., as well as *Cadetia*, *Diplocaulobium* and *Flickingeria*.
    III. A much smaller clade that consists of the genus *Epigeneium*.

    Following Clements (2003), these clades will here be referred to as the Asian, Australasian and *Epigeneium* clade respectively.
2. Under the consensus classification, *Dendrobium* is polyphyletic.

    Yukawa et al. (1993) found that the genus *Pseuderia* is not a member of the Dendrobiinae, but appears to belong to the tribe Podochileae. In view of the deviating vegetative and floral morphology of *Pseuderia*, both within Dendrobiinae and Podochileae, its placement within the subfamily Epidendroideae needs further study. In addition, Clements (2003) showed that a group of species traditionally treated as section *Oxystophyllum* of *Dendrobium* properly belongs in the subtribe Eriinae.

The taxonomic implications of these molecular studies found their expression in two highly divergent views. Some authors presented arguments in favour of a very large, monolithic and monophyletic genus *Dendrobium*, essentially comprising the whole subtribe Dendrobiinae, except perhaps the genus *Epigeneium* (Yukawa 2001, Burke et al. 2008). On the other hand, Clements & Jones (2002), in line with an earlier suggestion by Yukawa et al. (1993), proposed that *Dendrobium* should be split up in several smaller genera. Clements (2006) recognises as many as 50 genera in this alliance. According to Clements (2003), the three main clades should be treated as distinct subtribes (I: Dendrobiinae, II: Grastidiinae, and III: Epigeneiinae). Wood (2006), while provisionally following Dressler's consensus view (except for *Pseuderia* and *Oxystophyllum*), expressed the hope that a middle ground between extreme lumping and extreme splitting could be found.

Material and methods

The phylogram here shown (Fig. 1, 2) is based on sequences of the Internal Transcribed Spacer 1 (partial), 5.8S ribosomal RNA gene (complete), and Internal Transcribed Spacer 2 (partial) downloaded from GenBank (http://www.ncbi.nlm.nih.gov). See Table 1 for taxa and accession numbers. Taxa were selected to make the analysis comparable to earlier studies by Clements (2003, 2006) and Yukawa (2001). Where possible, different but morphologically similar species were chosen. When a taxon was represented by multiple accessions, initially all accessions were included

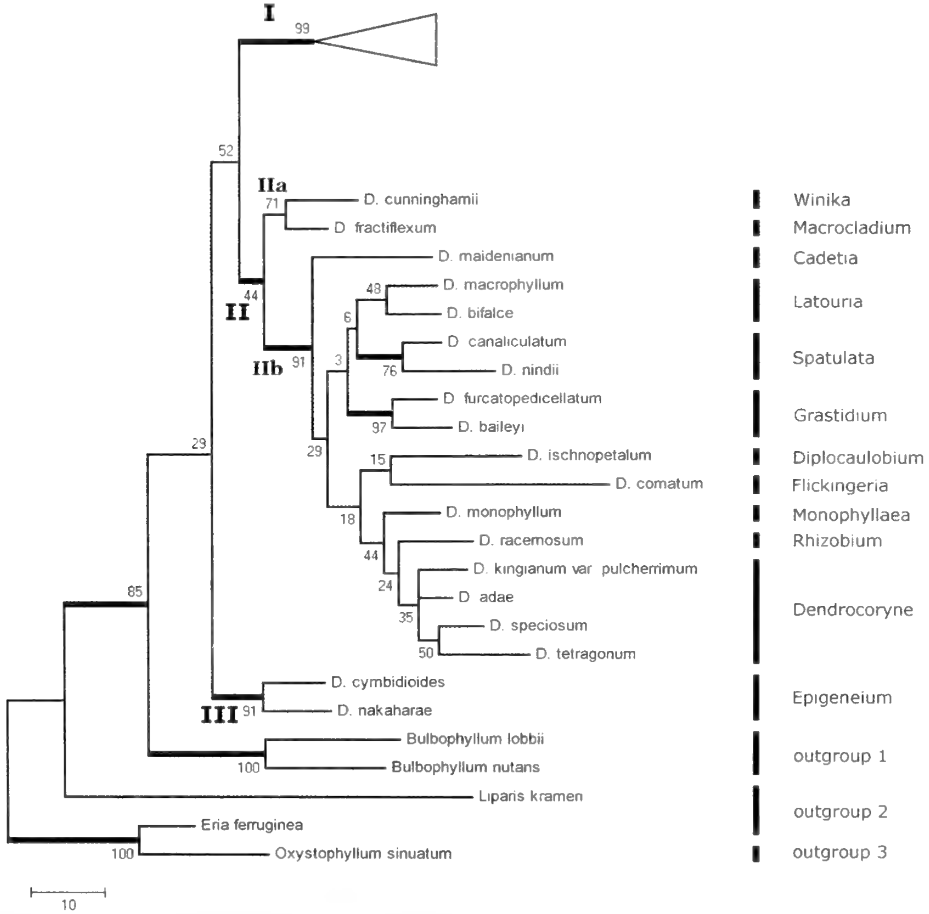

Fig. 1. One of 20 most parsimonious phylograms of selected *Dendrobium* species based on ITS sequence data. Names on the right refer to the traditional sections and genera in which the species would be included. Clade I is shown in Fig. 2.

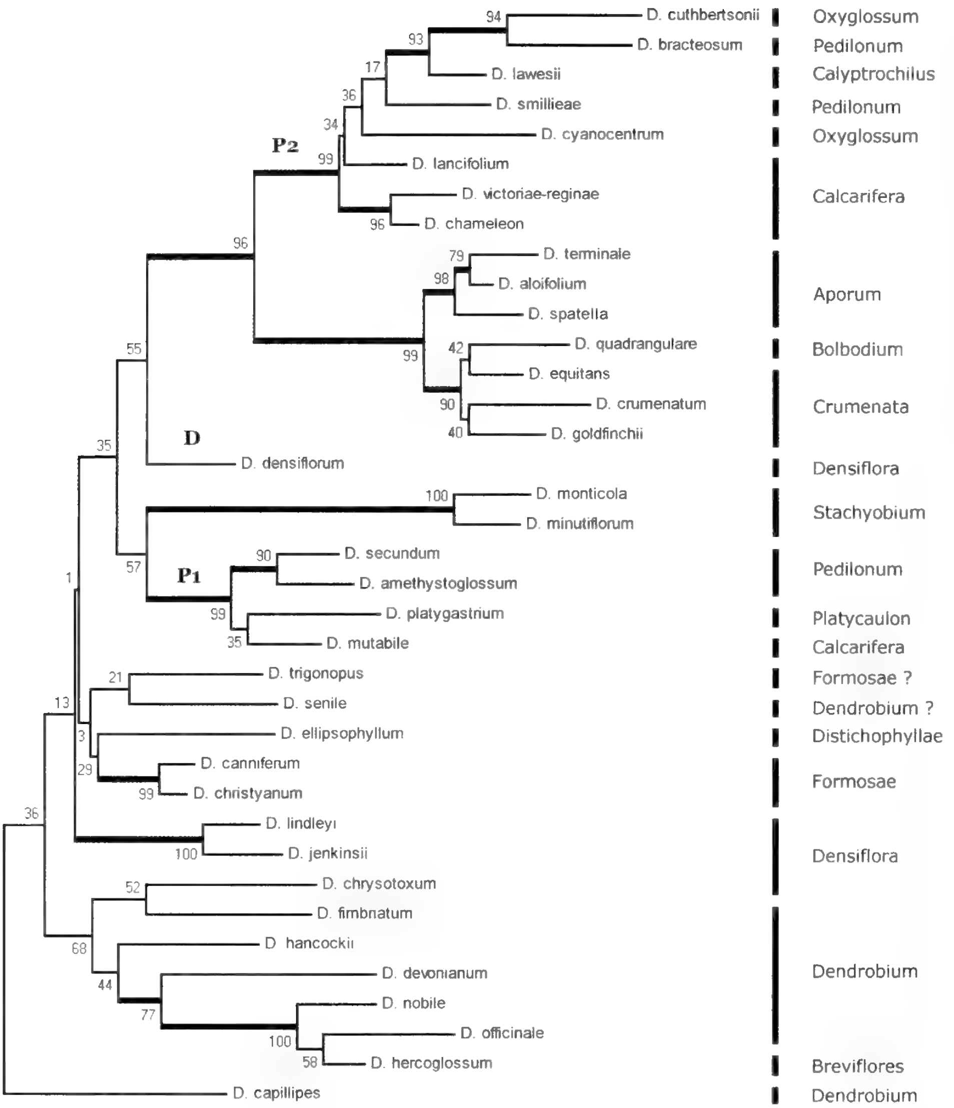

Fig. 2. Phylogram of Clade I (from Fig. 1).

in the alignment. In all cases these accessions gave identical results during phylogeny inference, although there often were minor differences between the sequences, for example in the three accessions of *D. chrysotoxum* Lindl. Afterwards one accession was chosen arbitrarily to represent the taxon. Unfortunately, Yukawa's and part of Clements's sequence data were not yet uploaded to GenBank at the time of this study.

A number of motif-based tests for the detection of pseudogenes were performed (Harpke & Peterson 2008, Feliner & Rosselló 2007). Sequences were aligned with Mega version 4 (Tamura et al. 2007), using the ClustalW algorithm, and adjusted manually. The phylogeny of the 61 selected taxa was inferred with Mega4, using maximum parsimony with the following options: close-neighbour interchange,

Table 1. List of GenBank accession numbers.

Bulbophyllum lobbii Lindl. – EF195931; *B. nutans* Thouars – EF196038; *Dendrobium adae* F.M.Bailey – EU430371; *D. aloifolium* (Blume) Rchb.f. – AY239951; *D. amethystoglossum* Rchb.f. – AY239952; *D. baileyi* F.Muell. – AY240016; *D. bifalce* Lindl. – EU430373; *D. bracteosum* Rchb.f. – AY239954; *D. canaliculatum* R.Br. – EU430375; *D. capillipes* Rchb.f. – AF362035; *D. cariniferum* Rchb.f. – AF362027; *D. chameleon* Ames – AF521607; *D. christyanum* Rchb.f. – EF629325; *D. chrysotoxum* Lindl. – EU477501; *D. comatum* (Blume) Lindl. – AB289469; *D. crumenatum* Sw. – AF521608; *D. cunninghamii* Lindl. – AY240019; *D. cuthbertsonii* F.Muell. – AY239950; *D. cyanocentrum* Schltr. – AY239964; *D. cymbidioides* (Blume) Lindl. – AY240011; *D. densiflorum* Wall. ex Lindl. – DQ058786; *D. devonianum* Paxton – FJ384735; *D. ellipsophyllum* Tang & F.T.Wang – AF362033; *D. equitans* Kraenzl. – AF521609; *D. fimbriatum* Hook. – EU003116; *D. fractiflexum* Finet – AY239949; *D. furcatopedicellatum* Hayata – AF521611; *D. goldfinchii* F.Muell. – AY239969; *D. hancockii* Rolfe – EU003120; *D. hercoglossum* Rchb.f. – AF363685; *D. ischnopetalum* Schltr. – AY240007; *D. jenkinsii* Wall. ex Lindl. – DQ058785; *D. kingianum* var. *pulcherimum* Rupp – EU430385; *D. lancifolium* A.Rich. – AY239976; *D. lawesii* F.Muell. – AY239977; *D. lindleyi* Steud. – DQ058784; *D. macrophyllum* A.Rich. – AY239979; *D. maidenianum* Schltr. – AY239948; *D. minutiflorum* S.C.Chen & Z.H.Tsi (= *D. sinominutoflorum* S.C.Chen, J.J.Wood & H.P.Wood) – DQ058800; *D. monophyllum* F.Muell. – EU430387; *D. monticola* P.F.Hunt & Summerh. – DQ058798; *D. mutabile* (Blume) Lindl. – AY239984; *D. nakaharae* Schltr. – AF521618; *D. nindii* W.Hill – AY239985; *D. nobile* Lindl. – EU477507; *D. officinale* Kimura & Migo (= *D. catenatum* Lindl.) – EU592018; *D. platygastrium* Rchb.f. – AY239955; *D. quadrangulare* Parish & Rchb.f. (= *D. hymenanthum* Rchb.f.) – EU840698; *D. racemosum* (Nicholls) Clemesha & Dockrill – EU430389; *D. secundum* (Blume) Lindl. – AY239993; *D. senile* Parish ex Rchb.f. – EU477509; *D. smillieae* F.Muell. – AY239996; *D. spatella* Rchb.f. – AF362034; *D. speciosum* Sm. – EU430399; *D. terminale* Parish & Rchb.f. – DQ058801; *D. tetragonum* A.Cunn. – EU430403; *D. trigonopus* Rchb.f. DQ058793; *D. victoriaereginae* Loher – EU840694; *Eria ferruginea* Lindl. – AF521071; *Liparis krameri* Franch. & Sav. – AB289469; *Oxystophyllum sinuatum* (Lindl.) M.A.Clem. – AY239995.

search level 3, with 50 random addition tree replications. Tree support was tested using bootstrapping with 1000 replications. Gaps were treated as missing data ('include all sites' option in Mega4). For various small subsamples of the taxa parsimony analyses were conducted using the exhaustive max-mini branch-and-bound algorithm in Mega4. These analyses produced tree topologies that were consistent with the ones found in the complete analysis.

Results

A. Testing for pseudogenes

Harpke & Peterson's test motif CGATGAAGAACGyAGC is not found in any species included in this study; all have CGATGAAGA**G**CGCAGC instead (absence of the test motif indicates potential pseudogene). On the other hand, the test motif GAATTGCAGAAwyC is present in all species except in *D. hancockii*, which has

AAATTGCAGAATCC. The motif GGCry-(4 to 7n)-GyGyCAAGGAA (Feliner & Rosselló 2007) was found only in *Eria ferruginea* Lindl., *D. mutabile* Blume and *D. maidenianum* Schltr. The motif GAATTGCAGAATTC, unlike the more general GAATTGCAGAAwyC recommended by Harpke & Peterson, was not found in any species, all had GAATTGCAGAATCC, except for *D. hancockii* Rolfe, which had AAATTGCAGAATCC. A conserved EcoRV site, GATAC, was not present in *D. nobile* Lindl., *D. officinale* Kimura & Migo (= *D. catenatum* Lindl.), *D. hercoglossum* Rchb.f., *D. victoriae-reginae* Loher and *D. chameleon* Ames; these all had GATAT. These results show that further testing for pseudogenes is indicated for all the species included in this study, and that at least the sequence for *D. hancockii* here used is likely to be a pseudogene. According to Burke et al. (2008) the inclusion of pseudogenes did not have a significant influence on the phylogeny inferred in their study, except that longer branch lengths were found as a result. They identified the sequence of their accession of *D. baileyi* F.Muell., also used in the present study, as a potential pseudogene. In theory, the use of paralogous sequences could influence the inferred phylogeny considerably. However, in *Dendrobium* strongly supported results using matK are usually replicated with strong support when using ITS (Wongsawad et al. 2005, Satthapattayanon 2008), and vice versa. This suggests that these results are not much distorted by the inclusion of pseudogenes, or paralogous sequences in general. The position of *D. hancockii* in Fig. 2 is in agreement with its membership of section *Dendrobium* on morphological grounds. Likewise, *D. baileyi* nests with another member of section *Grastidium*, as expected (Fig. 1). Nevertheless, the fact that quite a few species of *Dendrobium* are unplaced, as discussed below, may indicate that the role of pseudogenes and other genetic factors, such as ancient hybridization, need further study.

B. Phylogeny

The aligned sequences had a length of 747 sites (including gaps), of which 395 were parsimony informative. One of the 20 most parsimonious trees (length 2409, consistency index 0.404, retention index 0.619) is shown here (Fig. 1, 2). In its general topology it agrees well with earlier studies by Yukawa and co-workers (Yukawa 2001, Yukawa & Uehara 1996, Yukawa et al. 1993, 1996, 2000), Clements (2003, 2006) and Burke et al. (2008). In line with these studies, three main clades (marked I, II and III) can be distinguished in the ingroup. It is seen that *Cadetia*, *Flickingeria* and *Diplocaulobium* are all nested within the Australasian clade (II), demonstrating that recognition of these genera while maintaining *Dendrobium* in the broad sense renders the latter paraphyletic, as first noted by Yukawa et al. (1993). The Asian clade (I) generally shows longer branches than the Australasian clade. In the Asian clade the average number of changes from the nearest node common to clade I and II to a terminal node is 65.2; in the Australasian clade this is 28.9 changes.

The following discussion includes the results of the studies cited above. Some of the sections and species mentioned below are not found in the phylogram shown here because there were no sequences available from GenBank for these.

In contrast to most other studies, bootstrap support for the *Dendrobium* clade as a whole was here found to be low. No clear grounds for this anomaly could be detected. The *Epigeneium* clade (III) is well supported; it is basal to the two other clades, of which the Asian clade (I) has very strong bootstrap support here as well as in all studies cited. The Australasian clade (II) is less strongly supported, as is also seen in other studies. The basal dichotomy in the Australasian clade is again a result common to all studies. It represents a split between a clade (IIa) consisting of species from New Zealand and New Caledonia, traditionally included in section *Macrocladium* on the one hand, and a clade (IIb) consisting of numerous Australian/Asian species in many other sections on the other. Clements (2006) included a wider sample of New Caledonian species, showing that the sections *Macrocladium*, *Kinetochilus*, *Dendrobates*, *Inobulbum*, *Finetianthe* and *Tetrodon* are closely related, but the topology of the subtree is not well supported. The very limited sequence divergence at the higher nodes in this New Caledonian group hardly validates the recognition of so many sections. In Clements's analysis, the New Guinean *D. herpetophytum* Schltr. (section *Herpethophytum*) is nested deeply within this clade. In Yukawa's (2001) phylogram, on the other hand, an unidentified species of sect. *Herpethophytum* resides in a clade with sections *Grastidium*, *Pleianthe* and *Biloba* (syn. sect. *Monanthos*), which agrees much better with morphology and biogeography. As is evident from Clements (2006) and Yukawa (2001), most of the subclades within clade IIb correspond well with morphologically recognised sections, such as *Cadetia*, *Diplocaulobium*, *Brevisaccata* (syn. sect. *Trachyrhizum*), *Crinifera* (genus *Flickingeria*), and *Latouria*. The last, however, is not strongly supported, even when the anomalous position of *D. spectabile* (Blume) Miq. in Clements (2006) is disregarded. In the present study support for clade IIb is much stronger than it is in Clements (2006).

Sections *Spatulata*, *Phalaenanthe* and *Eleutheroglossum* together form a well supported clade that is consistent with morphology. It appears that at least sect. *Phalaenanthe* is nested within sect. *Spatulata* and may not warrant continued recognition.

Another strongly supported, morphologically and biogeographically plausible clade consists of sections *Grastidium* (including *Eriopexis* and *Dichopus*), *Biloba*, *Herpethophytum* and *Pleianthe*. Not enough species have been sampled to assess the robustness of the sections within this *Grastidium* clade, but the four mentioned here are easily distinguished morphologically.

Two species of section *Fugacia* (syn. sect. *Euphlebium*) were sampled by Clements (2006). Although this section is well-characterised by vegetative and floral morphology, the two species appear in two separate clades within clade IIb, but without strong support one way or the other.

Sections *Dendrocoryne*, *Monophyllaea* (syn. *Australorchis*) and *Rhizobium* were analysed in detail by Burke et al. (2008) and Adams et al. (2006). Their work suggests that, although morphologically distinct, sections *Rhizobium* and *Monophyllaea* are nested within a broadly defined sect. *Dendrocoryne*. Sect. *Rhizobium* seems to represent a recently evolved clade with xeromorphic adaptations (Yukawa et al. 2000).

Finally, still within clade IIb, Yukawa (2001) finds *D. bulbophylloides* Schltr. of sect. *Microphytanthe* to be sister to *Flickingeria*, but the clade combining these two has low bootstrap support. In Clements's (2006) phylogram *D. bulbophylloides* is sister to *D. toressae* (F.M.Bailey) Dockrill (sect. *Lichenastrum*), with the pair in turn sister to *Flickingeria*, but again with low support.

In summary, in the Australasian clade the sectional classification based on morphology is largely supported by the molecular phylogenies. The relationships between the clades are largely unresolved, however. The position of *Cadetia*, for example, is still unclear.

Turning to the Asian clade (I), the picture is much more confusing. There are several well supported clades, but also quite a few species that do not nest inside any of those clades, e.g., the closely related *D. lindleyi* Steud. and *D. jenkinsii* Wall. ex Lindl., *D. senile* Parish ex Rchb.f., *D. trigonopus* Rchb.f., and *D. capillipes* Rchb.f., which must all be considered unplaced at present. A broad sampling of the florally very similar sections *Dendrobium* and *Densiflora* (syn. sect. *Callista*) by Wongsawad et al. (2005) confirmed that sect. *Densiflora* is polyphyletic, as found by earlier studies (e.g., Yukawa 2001), with *D. chrysotoxum* deeply nested in a well-supported clade that contains species of sect. *Dendrobium* and sect. *Breviflores*. Two other clades of sect. *Densiflora* are each strongly supported, one consisting of the species pair *D. lindleyi* and *D. jenkinsii*, the other consisting of the relatives of *D. densiflorum* Wall. ex Lindl. (clade D in Fig. 2). However, the position of these clades within the Asian clade is still undetermined. It is hard to explain how the continental Asian *D. densiflorum* alliance could be sister to *D.* sect. *Amblyanthus*, a morphologically quite different section with a predominantly East Malesian distribution, and not to one of the much more similar clades from continental Asia. Yet, this is suggested by the analyses by Yukawa (2001), Wongsawad et al. (2005) and the ITS-based analysis of Sathapattayanon (2008), although not by her matK-based analysis. It should be noted that branch lengths inferred from ITS sequences in the *D. densiflorum* clade and in the *Amblyanthus* clade are much shorter (by about a factor 0.5) than in the neighbouring clades, for instance the second *Pedilonum* clade (clade P2 in Fig. 2) mentioned below. This could be a factor in explaining the rather counterintuitive position of clade D. Section *Dendrobium* is largely supported by Wongsawad et al.'s study, except for a few species (Wongsawad et al.'s clade 7, here represented by *D. capillipes* in Fig. 2) that form a small, rather inexplicably unplaced group outside the main *Dendrobium* clade. Section *Breviflores*, still according to Wongsawad et al., is polyphyletic, and should probably be included in sect. *Dendrobium*.

Section *Formosae* has recently been analysed in detail by Sathapattayanon (2008), who found that the section as traditionally circumscribed falls apart into two distinct sections next to two morphologically aberrant species that have to remain unplaced for the time being (*D. trigonopus* and *D. jerdonianum* Wight). The core of sect. *Formosae* forms a well-defined monophyletic group of some 40 species. The sections *Distichophyllae* and *Conostalix* are, according to ITS data, sister to the as-yet-unnamed clade split off from sect. *Formosae*, but not according to matK data.

Section *Stachyobium* is a strongly supported clade with high sequence divergence. Its position within the Asian clade varies more than any other subclade in the various studies here cited, and this morphologically distinctive section must be considered unplaced.

Perhaps the greatest problem in the Asian clade is presented by the species of the sections *Pedilonum*, *Calcarifera*, *Oxyglossum*, *Calyptrochilus*, *Platycaulon* and *Dolichophyllum*. It was generally believed that they formed a single, monophyletic alliance within *Dendrobium*. The work of Clements (2003, 2006) suggests, however, that this alliance consists, at the highest level, of two strongly supported clades that are not sister clades. To some extent, these two clades are supported by geography, with one clade, P1 in Fig. 2, being predominantly West Malesian (this clade includes the type species for sect. *Pedilonum*, *D. secundum* (Blume) Lindl.), and the other, P2 in Fig. 2, being predominantly East Malesian. However, section *Platycaulon*, which falls in the West Malesian clade, is well represented in East Malesia. There are few, if any, morphological characters that can serve to distinguish P1 and P2. Species of the sections *Pedilonum* and *Calcarifera*, as traditionally understood, are found both in clade P1 and in P2.

The sister clade to P2 is a strongly supported alliance consisting of the sections *Crumenata*, *Aporum*, *Strongyle* and *Bolbodium*. This clade is probably best considered as a single section (to be called *Aporum*), because species with virtually identical, ephemeral flowers occur in each of the four sections. There is some support, however, for a subdivision into two subgroups, one having stems with a few swollen internodes, the other having stems without any swollen internodes. Section *Bolbodium* is nested within sect. *Crumenata*, and appears to represent a case of vegetative reduction or neoteny. The *Aporum* clade and clade P2 together form a strongly supported clade in all studies.

In summary, the Asian clade contains several well-supported subclades, but these are much less congruent with morphology than in the Australasian clade, and the relations between the subclades are, in many cases, still unclear.

Discussion

Do these results, and the studies cited here, support the splitting up of *Dendrobium* into smaller genera? To some extent they do, in that the three basal clades in the Dendrobiinae would at first sight be good candidates for recognition at genus level. Not only are they well supported, there is also a distinct geographical signal present. Unfortunately, there appear to be no consistent morphological characters to distinguish between the Asian clade and the Australasian clade. Both groups, if recognised as separate genera, would be highly heterogenous and an identification key for these two entities would be too complex to be useful. Therefore, if splitting is considered desirable, then this has to occur at lower levels. But, as I have pointed out repeatedly above, the delimitation of several clades is still problematic. There are unplaced species, there are fragmented morphology-based sections, and there are strongly supported clades that, if recognised as genera, would be very hard to distinguish from other genera. There is, beyond the level of the three basal clades, no obvious way to split up *Dendrobium* into monophyletic genera.

Apart from these practical difficulties, there are several arguments that can be invoked in favour of, or against splitting. The main arguments in favour of splitting, mostly paraphrased from Clements (2003, 2006), are:

1. A very large genus of more than 1500 species is impractical; it makes species-identification more difficult and membership of such a large genus conveys little information about the characters of any particular species.
2. Many clades are very distinctive, and some have already been recognised at genus level for a long time, such as *Cadetia* and *Flickingeria*.
3. It is inconsistent to have numerous small genera in one large subtribe, such as the Aeridinae, and only one big genus in another, even larger one.
4. Splitting is unavoidable, because the group under consideration is polyphyletic.

These are some possible counter arguments:

1. A large genus may be impractical, but so is a large number of genera that are difficult to distinguish.
2. Many clades are not distinctive at all.
3. There are no rules for the size of genera. The size of a genus depends on a specific, historical pattern of speciation and extinction, therefore a wide range of sizes among different genera is to be expected. Moreover, the number of recognised genera in the Aeridinae is probably far too large.
4. After the removal of *Pseuderia* and *Oxystophyllum*, the polyphyly argument no longer applies to *Dendrobium*.

The main arguments against splitting are as follows:

1. There is no obvious 'best' way to split *Dendrobium* into smaller genera.
2. Splitting is at any rate premature because the presently available phylogenies show too little resolution, and the sampling has been inadequate for most sections.
3. While many of the segregate genera are easily recognised (*Cadetia*, *Diplocaulobium*), others would be hard to distinguish, even by specialists.
4. Splitting will result in a huge number of name changes, rendering older publications obsolete and herbarium management more difficult. Reassigning *Cadetia* and other segregates back to *Dendrobium* will do this to a far lesser extent.
5. The horticulturally extremely important *D. bigibbum* and its hybrids will no longer belong to the genus *Dendrobium*.
6. The popular image of taxonomists as people who endlessly tamper with well-established names will be confirmed.

All arguments considered, and recognising that one of the few objective criteria that may guide us in the delimitation of genera is the criterion of monophyly, it seems to me preferable to take a broad view of *Dendrobium*, and to include in it all the former segregate genera (except *Pseuderia* and *Oxystophyllum*). In principle, the genus *Epigeneium* could be kept as a separate genus, as it is sister to all the other species in the Dendrobiinae. However, morphologically *Epigeneium* is not particularly distinctive when compared with such species as *Dendrobium carrii* Rupp & C.T.White.

Inclusion of *Epigeneium* would not add any new character states, or even any obvious combinations of character states to *Dendrobium*. Therefore, apart from its status as sister genus, there are hardly any solid arguments to maintain this relatively small genus of some 40 species next to the huge conglomerate of *Dendrobium*. There is also no particularly large sequence divergence between *Epigeneium* and the rest of *Dendrobium*.

The case of *Dendrobium* is not unique; similar problems are posed by other very large orchid genera including *Bulbophyllum*, *Epidendrum*, *Eria*, *Habenaria*, and *Pleurothallis*, among others. In the case of *Eria* and *Pleurothallis*, the arguments in favour of splitting have prevailed (Pridgeon et al. 2005), and in my opinion rightly so, since the formerly broadly defined genera were clearly highly polyphyletic. Generic delimitation is still debatable in some cases. Splitting of *Epidendrum* (Pridgeon et al. 2005) and *Bulbophyllum* (Vermeulen, pers. comm.) has so far not been favoured by modern experts in these genera. At least in the case of *Bulbophyllum*, the arguments are very much like those listed above for *Dendrobium*, except that *Bulbophyllum* has far less significance in horticulture.

Character evolution and the origin of Dendrobium

Roughly speaking, there are two main habit types in *Dendrobium*: plants with pseudobulbs and plants with cane-like stems. This is an oversimplification, as there are many intermediate cases, but it does raise the question what the earliest dendrobiums looked like. I believe the molecular phylogenies enable us to answer this question. We now know that the *Epigeneium* clade is sister to all the other *Dendrobium* species, and we also know that *Bulbophyllum* is sister to *Dendrobium s.l.* All *Bulbophyllum* species have heteroblastic pseudobulbs with one or two, non-sheathing apical leaves. The same is true for *Epigeneium*. Moreover, *Epigeneium* has distinct, creeping rhizomes, a character-state also found in numerous *Bulbophyllum* species. These facts suggest that the earliest dendrobiums were plants with heteroblastic pseudobulbs with one or two terminal, non-sheathing leaves and creeping rhizomes. Species, indeed whole sections, with such a habit are still found in the Australasian clade, for example in sections *Diplocaulobium*, *Rhizobium*, *Microphytanthe*, and others. However, they are not basal in this clade, and are absent from the Asian clade. This suggests that the most recent common ancestor to the Asian and Australasian clade was a plant with a cane-like habit, and that cases like *Diplocaulobium* represent reversals to the earliest ancestral type.

How early were those earliest ancestors? There are various theories about the origin of *Dendrobium*. The clear split between an Asian and an Australasian clade (or what Wood (2006) refers to as the Northern and Southern clade) has led some authors (Brieger 1981, Wood 2006) to propose a very early origin for *Dendrobium*, as they invoke the splitting up of Gondwanaland (around 60–70 million years ago) to explain the existence of the two clades. However, if that were the case, then one would expect far greater sequence as well as morphological divergence between the two clades than is actually observed. A more recent origin in continental Asia, or possibly Africa, with subsequent dispersal to Australia, New Caledonia and New Zealand, as advocated by Lavarack et al. (2000), seems more plausible. Dispersal in the opposite direction would explain why certain members of the Australasian clade are in fact better represented in the western (Asian) part of the range of *Dendrobium*, in particular sect. *Crinifera* (the former genus *Flickingeria*). The radiation of clade P2 in New Guinea may be the result of a relatively recent secondary west-to-east dispersal. The complex geology of Wallacea, with land rapidly appearing and disappearing within a few million years around 10 million years ago (Hall 2009), may explain these secondary dispersals. As for the primary dispersal from Asia to Australia, New Caledonia, and New Zealand, this must have occurred more than 23 million years ago, assuming that a recently discovered, c. 23 million year old fossil from New Zealand described as *D. winikaphyllum* Conran, Bannister & Lee (Conran et al. 2009), is indeed a *Dendrobium* species. Gustaffson et al. (2010), using this fossil to provide a calibration point, dated *Dendrobium* to about 32 mya, with a 95% confidence interval of 25 to 40 my.

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Implications from molecular phylogenetic data for systematics, biogeography and growth form evolution of *Thottea* (Aristolochiaceae)

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ABSTRACT. The genus *Thottea* comprises about 35 species distributed from India throughout Southeast Asia. However, most of the species have a narrow distribution. A first molecular phylogeny based on the chloroplast *trnK* intron, *matK* gene and *trnK-psbA* spacer is presented and confirms the monophyly of the genus according to Hou in 1981. Earlier subdivisions into the sections or genera *Apama* and *Thottea* could not be substantiated since both proved to be paraphyletic with respect to each other. The taxonomic and systematic history of *Thottea* is discussed with respect to molecular and morphological data. *Thottea piperiformis* is sister to all other species, which gives limited recognition to *Asiphonia piperiformis* as proposed by Huber (1985). *Thottea tomentosa*, one of the smallest and most widespread species is subsequently sister to all remaining species. *Thottea* diversified in two biogeographic regions: the Western Ghats in India and the Indo-Malayan region. A high degree of endemism is observed resulting from the presence of very few species shared between islands, which might be the result of a single colonisation and subsequent radiation. Within Piperales, *Thottea* holds a key position between the herbaceous Asaroideae and the woody Aristolochioideae.

Keywords. Aristolochiaceae, biogeography, growth form evolution, molecular phylogeny, Thottea

Introduction

During the last two centuries, the number of accepted genera within Aristolochiaceae has differed according to the dataset investigated (e.g., seven by González & Stevenson 2002; five by Neinhuis et al. 2005 and Ohi-Thoma et al. 2006). Currently, the family Aristolochiaceae is divided into two subfamilies Aristolochioideae and Asaroideae and four genera are consistently recognised (*Saruma* Oliv., *Asarum* L., *Thottea* Rottb.

and *Aristolochia* L.) (Wanke et al. 2007a). However, Aristolochiaceae has turned out to be paraphyletic with respect to *Lactoris fernandeziana* Phil. and probably also Hydnoraceae (Nickrent et al. 2002; Wanke et al. 2007a), which will not be addressed here further. The subfamily Asaroideae contains small-sized herbaceous plants with flowers characterised by an actinomorphic perianth. It consists of two genera: the monotypic *Saruma* (*S. henryi* Oliv.), endemic to central China (Zhou et al. 2010) and *Asarum* with about 86 species from temperate areas of North America, Europe and Asia (Kelly 1998, Kelly & Gonzalez 2003, Wanke et al. 2006a). In contrast, the Aristolochioideae are distributed from tropical to temperate climate zones (Neinhuis et al. 2005). *Thottea* includes about 35 shrubby species with an actinomorphic perianth restricted to tropical Asia, while *Aristolochia* is the most species-rich genus with about 400 species representing geophytes, perennial herbs, climbers and shrubs (Wanke et al. 2006a).

Most likely due to the lack of *Thottea* in *ex situ* collections, only a few species have ever been included in molecular-based phylogenetic studies (e.g., Neinhuis et al. 2005, Ohi-Thoma et al. 2006, Wanke et al. 2006a, 2007a). However, all studies have assumed the monophyly of the genus based on morphological characters. In addition, traditional taxonomic concepts and infrageneric relationships have not yet been addressed using molecular data.

Since the genus *Thottea* was described by Rottböll (1783) seven further genera have been published and used by later authors at tribal or sectional levels:

Thottea Rottb. (type: *T. grandiflora* Rottb.), Nye Dansk. Vidensk. Selsk. Skrift. ii. (1783) 529. I. 2;
Apama Lam. (type: *A. siliquosa* Lam.), Encycl. (Lamarck) 1(1). (1783) 91;
Bragantia Lour. (type: *B. racemosa* Lour.), Fl. Cochinch. 2. (1790) 528;
Ceramium Blume (type: *C. tomentosum* Blume), Bijdr. Fl. Ned. Ind. 17. (1826-27) 1134, nom. illeg.: renamed as *Munnickia* Rchb., Consp. Regn. Veg. 85 (1828), *Vanhallia* Schult.f., Syst. Veg. 7 (1829) xviii &166, and *Cyclodiscus* Klotzsch, Monatsb. Akad. Berl. (1859) 591.
Trimeriza Lindl. (type: *T. piperina* Lindl.), Edwards's Bot. Reg. 18. (1832) sub t. 1543;
Asiphonia Griff. (type: *A. piperiformis* Griff.), Trans. Linn. Soc. London 19. (1845) 333, t. 37;
Lobbia Planch. (type: *L. dependens* Planch.), London J. Bot. 6. (1847) 144, t. 3;
Strakaea C.Presl. (type: *S. melastomaefolia* C.Presl.), Epimel. Bot. (1851) 221;

Different taxonomic concepts are shown in Table 1. Klotzsch (1859) accepted three genera in two tribes, while Duchartre (1864) recognised only two: *Thottea* and *Bragantia*, and put all other genera in synonymy. He distinguished both genera by the number and arrangement of stamens. Whereas *Thottea* possesses 16–36 stamens arranged in two whorls (e.g., *T. abrahamii* M.Dan, P.J.Mathew, Unnithan & Pushp., Fig. 1A), *Bragantia* exhibits one whorl with only 6 to 10 stamens (e.g., *T. barberi* (Gamble) Ding Hou, Fig. 1B). Hooker adopted this classification but noted that both genera might "well be united" (Hooker 1890) because of their morphological similarity. Solereder (1894) also accepted the division into two genera but renamed *Bragantia*

Table 1. Traditional and current taxonomic concepts of the genus *Thottea* s.l.

Klotzsch (1859)	Duchartre (1864)	Hooker (1890)	Solereder (1894)	Hou (1981)	Huber (1985)
Tribus Bragantieae					
Thottea Rottb. incl. *Lobbia* Planch.; *Thottea* Rottb.	*Thottea* Klotzsch sect. I: THOTTEA incl. *Thottea Rottb.* sect. II: LOBBIA incl. *Lobbia* Planch.	*Thottea* Rottb. incl. *Lobbia* Planch.; *Thottea* Rottb.	*Thottea* Rottb. incl. Lobbia Planch.; *Thottea* Rottb.	*Thottea* Rottb. incl. *Apama* Lam.: *Asiphonia* Griff.; *Bragantia* Lour.; *Ceramium* Blume; *Cyclosdiscus* Klotzsch; *Lobbia* Planch.; *Strakaea* C.Presl.; *Thottea* Rottb.; *Trimeriza* Lindl.	*Thottea* Rottb. sect. THOTTEA sect. APAMA
Bragantia Lour. incl. *Asiphonia* Griff.; *Bragantia* Lour.; *Trimeriza* Lindl.	*Bragantia* Lour. sect. I: EUBRAGANTIA incl. *Asiphonia* Griff.; *Bragantia* Lour.; *Strakaea* C.Presl. sect. II: TRIMERIZA incl. *Apama* Lamk.; *Trimeriza* Lindl.	*Bragantia* Lour. incl. *Asiphonia* Griff.; *Apama* Lamk.; *Bragantia* Lour.; *Ceramium* Blume; *Cyclodiscus* Klotzsch; *Strakaea* C.Presl.; *Trimeriza* Lindl.	*Apama* Lam. sect. I: BRAGANTIA incl. *Asiphonia* Griff.; *Bragantia* Lour.; *Strakaea* C.Presl. sect. II: TRIMERIZA incl. *Apama* Lamk., *Trimeriza* Lindl.		*Asiphonia* Griff.
Tribus Cyclodiscineae					
Cyclodiscus Klotzsch incl. *Ceramium* Blume; *Cyclodiscus* Klotzsch	sect. III: CYCLODISCUS incl. *Ceramium* Blume; *Cyclodiscus* Klotzsch		sect. III: CYCLODISCUS incl. *Ceramium* Blume; *Cyclodiscus* Klotzsch		

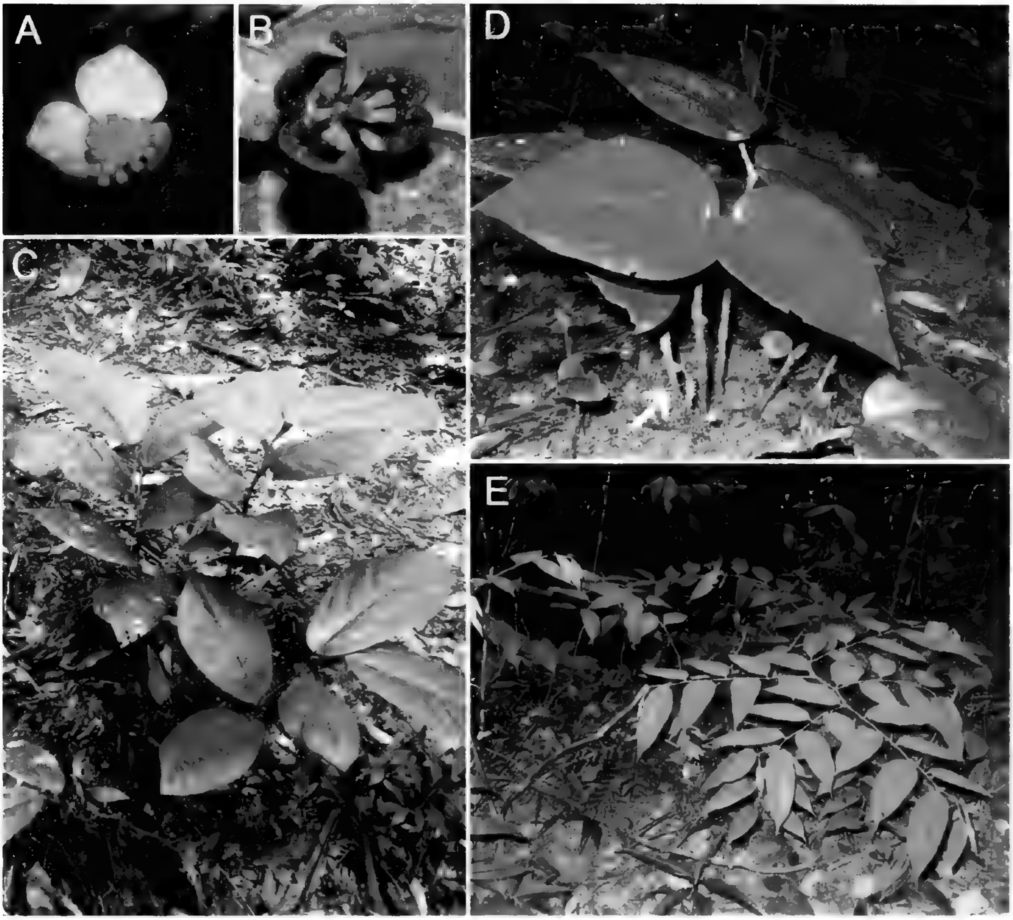

Fig. 1. Diversity of flowers and vegetative organisation within *Thottea* s.l. (Hou 1981). **A.** Flower of *T. abrahamii* M.Dan, P.J.Mathew, Unnithan & Pushp. (sect. *Thottea*) with stamens arranged in two whorls. **B.** Flower of *T. barberi* (Gamble) Ding Hou (sect. *Apama*), possessing 9 stamens in one whorl. **C.** Growth habit of *T. grandiflora* Rottb. **D.** *T. tomentosa* (Blume) Ding Hou, reaching only 40 cm in height. The flowers of this species appear at ground level (indicated by an arrow). **E.** *T. piperiformis* (Griff.) Mabb., growing up to 2 m or more with flowers borne in the axils of leaves. In addition to seed anatomy (Huber 1985), *T. piperiformis* also differs in growth form from all other species of the genus by its acrotonic branching.

as *Apama*, since this is the older name and has priority. About a century later, Hou published the most comprehensive study on the genus *Thottea* so far (Hou 1981). His study revealed that the differentiating characters of both genera were highly variable within species and even within one specimen. Based on these results he merged *Thottea* and *Apama* into one large genus *Thottea*. Furthermore, he explicitly pinpointed that no infrageneric subdivision is needed. A few years later, Huber (1985) again excluded one species, *Asiphonia piperiformis* Griff., due to the conspicuous seed anatomy. More recently six new species were described from India (Swarupanandan 1983; Sivarajan, 1985; Sivarajan & Babu 1985; Pandurangan & Nair 1993; Dan et al. 1996; Kumar et al. 2000). Although the flower and inflorescence morphology of the new Indian species were investigated from a systematic perspective (Shajiu & Omanakumari 2009, 2010), no further comprehensive study on the whole genus *Thottea* has been performed since then.

The aims of this study are to 1) test the monophyly of the genus *Thottea* sensu lato (s.l.) (Hou 1981) based on about half of the described species; 2) compare the most recent taxonomic concepts of Hou (1981) and Huber (1985), namely the treatment of the species as one single genus *Thottea*, and the separation of *Asiphonia* with the subdivision of the genus into the sections *Apama* and *Thottea* (Duchartre 1864), by means of molecular phylogenetic approaches; 3) compare results of a molecular phylogeny of the Indian species with the recently published results on flower and inflorescence morphology; and 4) provide a first molecular phylogenetic hypothesis as a starting point for more detailed studies addressing biogeographical questions, character evolution with respect to growth forms in *Thottea* and Aristolochiaceae and a revision of the genus reflecting natural relationships.

Methods

For this study, full sequences of three chloroplast regions (*trnK* intron, *matK* gene and *trnK-psbA* spacer) were generated for 15 *Thottea* species, as well as 21 species representing the other lineages of Aristolochiaceae and 3 outgroup genera of Saururaceae. For the latter, sequences of the *trnK* intron and the *matK* gene were derived from earlier studies (Wanke et al. 2006a, b, 2007a), whereas the *trnK-psbA* spacer was sequenced for this study. In Appendix A the origin of the material, voucher information and botanical garden accession numbers as well as GenBank accessions are provided. Total genomic DNA was isolated from herbarium specimens or leaves collected from the field or botanical gardens and dried in silica gel. A double-extraction approach with CTAB was used according to Borsch et al. (2003). After precipitation in ethanol and resuspension of the pellets in TE, DNA was cleaned by using the NucleoSpin® Extract II-Kit (Macherey-Nagel).

The amplification of the entire gene cluster was performed in one part for silica-dried material or in three parts with several 100 bp overlap for material from herbarium specimens. Primer sequences for amplification and sequencing are listed in Table 2. PCR products were obtained using a 25 µl reaction containing 1 µl template, 15.3 µl ddH_20, 2.5 µl 10x Taq buffer (15 mM $MgCl_2$), 1 µl of 25 mM $MgCl_2$, 0.5 µl of each primer (10 pmol/µl), 4 µl dNTP mix (1.25 mM each), 0.2 µl Taq DNA polymerase (Promega). Amplification conditions were: one cycle of 1.5 min at 96°C, 1 min at 50°C, 2 min at 68°C, 34 cycles of 0.5 min at 95°C, 1 min at 48°C, 2 min at 68°C, and a final extension of 20 min at 68°C in a T3 Thermocycler (Biometra). PCR products were purified and extracted from a 1.2% agarose gel, using the NucleoSpin® Extract II-Kit. Sequences were run with an in-house Beckman Coulter 8000 capillary sequencer or sent to Macrogens' sequencing service (Macrogen Inc., Korea).

Table 2. Amplification and sequencing primers used.

Primer name	Direction	Sequence (5'-3')	Design	Primer used for
trnK-F	forward	GGG TTG CTA ACT CAA TGG TAG AG	Wicke & Quandt (2009)	all taxa
psbA-R	reverse	CGC GTC TCT CTA AAA TTG CAG TCA T	Steele & Vilgalys (1994)	all taxa
AR-matK-2400R	reverse	ATT TTC TAG CAT TTG ACT CC	Wanke et al. (2007a)	*Aristolochia*
AR-matK-2660F	forward	CTT ATG ATG AAG AAA TGG AAA TA	this study	*Aristolochia*
AR-psbA-3720R	reverse	CCC ATT TGY TAT TTC GGA T	this study	*Aristolochia*
AR-trnK-3480F	forward	ATT CTG AAA TGT TTA CRC AGT AGT	this study	*Aristolochia*
Th-matK-1510R	reverse	TAA ACT CCT GAA AGA GAA GTG G	this study	*Thottea*
Th-matK-2000F	forward	TTA TGG GCT ATC TTT CAA GTC G	this study	*Thottea*
Th-matK-2190R	reverse	TAT CAG AAT CAG ACG AAT CGG C	this study	*Thottea*
Th-matK-910F	forward	GAC TGT ATC GCA CTA TGT ATC G	this study	*Thottea*

Sequences were manually edited and aligned using the *Phylogenetic Data Editor* PhyDE® v0.995 (www.phyde.de) following alignment rules proposed by Kelchner (2000) and Borsch et al. (2003). Sixteen hotspots were excluded from the original dataset prior to the phylogenetic analyses due to ambiguous homology assessments. The dataset contained two inversions, one in the genus *Thottea* s.l. and one in *Asarum* and *Saruma*. To use both for phylogenetic reconstruction, the information on presence/absence of the inversion as well as the mutational events within, the inversions were coded in two additional columns at the end of the alignment and reversed in the alignment. Subsequently, indels were automatically coded using the simple indel coding approach according to Simmons & Ochoterena (2000) as implemented in SeqState (Müller 2005a), a PhyDE® plugin. The alignment and the indel matrix are available from TreeBASE (www.treebase.org). For phylogenetic reconstruction Maximum Parsimony and Bayesian Inference methods were employed. The most parsimonious trees where obtained by using the parsimony ratchet (Nixon 1999), as implemented in PRAP2 (Müller 2005b). Ratchet settings were set at 20 random addition cycles of 500 ratchet replicates up weighting randomly 25% of the characters during each iteration. A strict consensus tree was calculated and nodes were evaluated by bootstrapping

(BS) in PAUP* v.4.0 (Swofford 2002) using 1000 replicates. MrBayes v3.1 (Ronquist & Huelsenbeck 2003) was utilised for Bayesian Inference analysis. The GTR + Γ + I model was applied for sequence data, and the restriction site model ("F81") for the indel matrix after testing the best fitting model using jModeltest 0.1.1 (Posada 2008). Ten independent runs with 1,000,000 generations and 4 chains each were run simultaneously. Every 100th generation of each run was collected. The burnin was evaluated using Tracer v1.5 (Drummond & Rambaut 2007). A consensus tree and the posterior probabilities (PP) were calculated after discarding the first 50,000 sampled generations of each run as burnin.

Results

Characterisation of the molecular dataset

The total length of the alignment comprises 4440 bp, the mean sequence length 2887 bp (min = 2730 bp, max = 3272 bp), while the mean sequences in *Thottea* had a length of 2806 bp (min = 2763 bp, max = 2821 bp). Two inversions were detected. One in *Thottea* (position 226 to 253 in the *trnK* intron) forming a hairpin with a poly-T microsatellite as terminal loop (Wanke et al. 2007a) and one in *Asarum* and *Saruma* (position 4178 to 4185 in the *trnK-psbA* spacer). The dataset exhibited a large number of length mutations (indels), 222 of which were identified by SeqState. The combined data matrix (excluding hotspots) comprised a total number of 3802 characters, 1361 of which were variable and 906 parsimony-informative.

Phylogenetic reconstruction

The phylogram obtained by Bayesian Inference is shown in Fig. 2. Maximum Parsimony (MP) analyses resulted in 18 most-parsimonious trees of 2248 steps (CI = 0.736, RI = 0.901). The topology of the Bayesian and the MP strict consensus tree are virtually identical among early nodes and therefore only one tree is shown. However, within *Thottea* s.l. differences in branching patterns are observed for nodes lacking statistical support.

All *Thottea* species sampled form a single clade, which has maximum statistical support in both MP and Bayesian analyses (Fig. 2), as well as the sister group relationship of *Thottea* to *Aristolochia*. *Thottea piperiformis*, which Huber (1985) separated from *Thottea* as a monotypic genus (*Asiphonia piperiformis),* appears as sister to all other *Thottea* species. *Thottea tomentosa*, the most widespread species, is subsequent sister to the remaining species (PP 0.99, BS 97). The remaining species are found in two main clades. One is statistically highly supported (PP 1.00, BS 100), containing all Southeast Asian species, whereas the other is statistically unsupported and contains all Indian species. Within the clade of Indian species *T. abrahamii* and *T. dinghoui* are branching first, followed by *T. barberi*. *Thottea ponmudiana* is subsequent sister to the remaining species. Relationships among the rest are statistically supported for *T. dalzellii* being sister to *T. sivarajanii*, but their sistergroup relationship to *T. siliquosa*, *T. idukkiana*, *T. duchartrei* and a yet unidentified accession is unsupported.

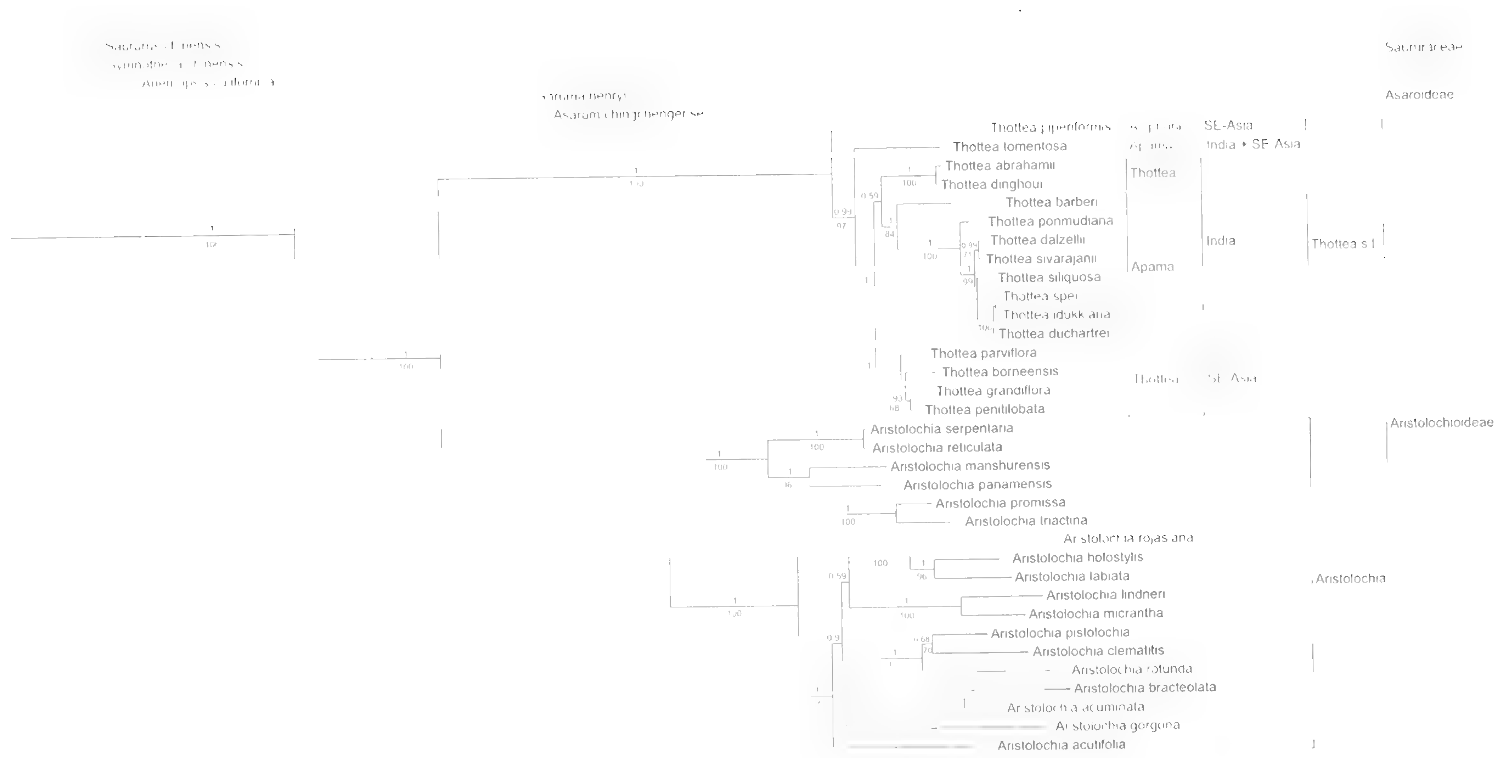

Fig. 2. Phylogram derived from Bayesian analysis, based on the chloroplast *trnK-matK-psbA* region, including coded length mutations. Posterior probabilities (PP) are given above and bootstrap values (BS) obtained from Maximum Parsimony analysis are shown below the branches. Probability values less than 0.5 and 50 for Bayesian and Maximum Parsimony, respectively, are not assigned. Branches interrupted by '//' represent only 50 percent of the actual substitution rate observed. The subgeneric classification within *Thottea* s.l. (Hou 1981) represents the generic concepts of Duchartre (1864) and Huber (1985). The recently described species from India were assigned to these three groups based on their morphology.

The Southeast Asian clade contains four species (*T. parviflora, T. borneensis, T. grandiflora* and *T. penitilobata*).

Discussion

Monophyly of Thottea and taxonomic concepts

Phylogenetic analyses, based on half of the currently accepted species, demonstrate that *Thottea* s.l. is monophyletic. The study includes a small but biogeographically representative selection of the Southeast Asian species, as well as a complete taxon sampling of the Indian species, which were newly described since the last revision of *Thottea* by Hou in 1981. Furthermore, the specimens studied represent all traditional taxonomic subdivisions and all the morphological diversity of the genus. Therefore the systematic concept of Hou (1981) based on morphology is substantiated as well as the assumption of Hooker (1890), that both genera, *Apama* and *Thottea*, "*...may well be united...*".

We assigned species published after the treatment of Hou (1981) and Huber (1985) to the respective sections based on morphological characters that have traditionally been used to delimit the sections. Both sections are paraphyletic with respect to each other. Although the relationships between the different *Apama* and *Thottea* representatives are not highly supported in all nodes, a broader sampling or better resolution will not achieve monophyly. Consequently, the morphological characters used by Duchartre (1864), i.e. the number and arrangement of the stamens, are a result of parallel evolution. It is well known that the number of floral organs in basal angiosperms is not strictly determined (Soltis et al. 2009; Chanderbali et al., in press) and might therefore be of less systematic value at the species level. *Thottea* shows a comparatively high variability of flowers and especially a high plasticity of the androecium (Hou 1981, Leins et al. 1988, Shajiu & Omanakumari 2010). Whereas in earlier studies only two stamen whorls have been proposed, the detailed study of Hou (1981) revealed up to four whorls. Hou (1981) found 6 to 46 stamens and 2 to 20 styles per flower. Both, the number of styles and stamens per flower have been shown to vary between different individuals of the same species and even within one single individual (Hou 1981, Shajiu & Omanakumari 2010). However, species with low stamen numbers tend to have a lower stamen variability (e.g., *T. duchartrei*, 8–10 stamens) or the number is even constant (e.g., *T. tomentosa* 6 stamens), whereas in species with higher stamen numbers greater variability is observed (e.g. *T. dinghoui*, 15–30 stamens) (Hou 1981, Shajiu & Omanakumari 2010).

The sister relationship of *T. piperiformis* (Fig. 1E) to all other *Thottea* species (Fig. 2) may appear to lend support to the treatment by Huber (1985), who segregated this species from *Thottea* s.l. under its former name *Asiphonia piperiformis*. However, after comparing the sequences, the number of substitutions is not higher than in other *Thottea* species (Fig. 2). We therefore follow Hou (1981) in accepting only one single genus *Thottea* including *Asiphonia piperiformis*.

Morphological characters of the flowers and inflorescences investigated by Shajiu & Omanakumari (2009, 2010) substantiate the relationships within the Indian species complex. The sister group relationship of *Thottea abrahamii* and *T. dinghoui* to the remaining species is characterised by a racemose inflorescence and bi-lobed floral bracts (Shajiu & Omanakumari 2009) as well as a high number of (15–39) dorsifixed stamens that are arranged in two whorls (Shajiu & Omanakumari 2010). In contrast, all other Indian species show cymose inflorescence patterns (Shajiu & Omanakumari 2009) as well as a lower number of (mostly 9) ventrifixed stamens arranged in one whorl (Shajiu & Omanakumari 2010). The segregation of the next clade, *T. barberi*, is supported by the equal distribution of the stamens around the styles, whereas a pattern of 3+3+3 stamens substantiates the relationship of *T. duchartrei, T. idukkiana, T. ponmudiana, T. siliquosa* and *T. sivarajanii*. The close relationship of the latter five is also confirmed by the presence of a gynostemium that, in contrast, is absent in *T. abrahamii, T. dinghoui* and *T. barberi*. Furthermore, the affinity of *T. idukkiana* and *T. duchartrei* is retrieved in terms of the following morphological characters of their flowers and inflorescences: the very small prophyll in comparison to the floral bracts, fused sepals, the presence of sterile appendages on the gynostemium that are assumed to be staminodes and the co-occurrence of entire as well as bifid stylar lobes (Shajiu & Omanakumari 2009, 2010). A morphological investigation of the undetermined species, which is cultivated in the Botanical Garden, Dresden, and resolved in the phylogeny together with *T. idukkiana* and *T. duchartrei*, revealed—besides a few differences—a high affinity to *T. idukkiana*. However, it has been used erroneously in our former studies as *T. siliquosa* (Neinhuis et al. 2005; Wanke et al. 2006a; Wanke et al. 2007a, b).

Outlook on biogeography and growth form evolution

From a biogeographic point of view, *Thottea* possibly represents an interesting case to study Southeastern Asian biogeography west of the Wallace line (Wallace 1859, 1863), as well as floristic affinities of this region to the Western Ghats in India, and island biogeography in general (Fig. 3). At first sight, the distribution of the genus seems rather constrained: from India to the Philippines and to the Greater Sunda Islands including one species crossing the Wallace line to Sulawesi (*T. celebica*). It is clear that *Thottea* diversified in two biogeographic regions: the Western Ghats in India and the Malesian region. In addition, a comparison of the biodiversity, distribution and similarity of species across the Islands, indicates that in most cases, only one species is shared between them, resulting in a high degree of endemism. Exceptions to this include only Sumatra, the Malay Peninsula, and Kra Isthmus, which share four species. However, floristic similarities of Sumatra and Malay Peninsula (Welzen et al. 2005) as well as Kra Isthmus and Malay Peninsula (Woodruff 2003) are well known. *Thottea tomentosa* (Fig. 1D) presents the link between the Indian species and the Southeast Asian species (excluding *T. piperiformis*). It is the smallest shrub within the genus that normally bears only 2 or 3 leaves per stem and is found throughout the western distribution area of the genus. Recently, Sumathi et al. (2004) reported the occurrence of *T. paucifida* from the Andaman Islands (not sampled in this study).

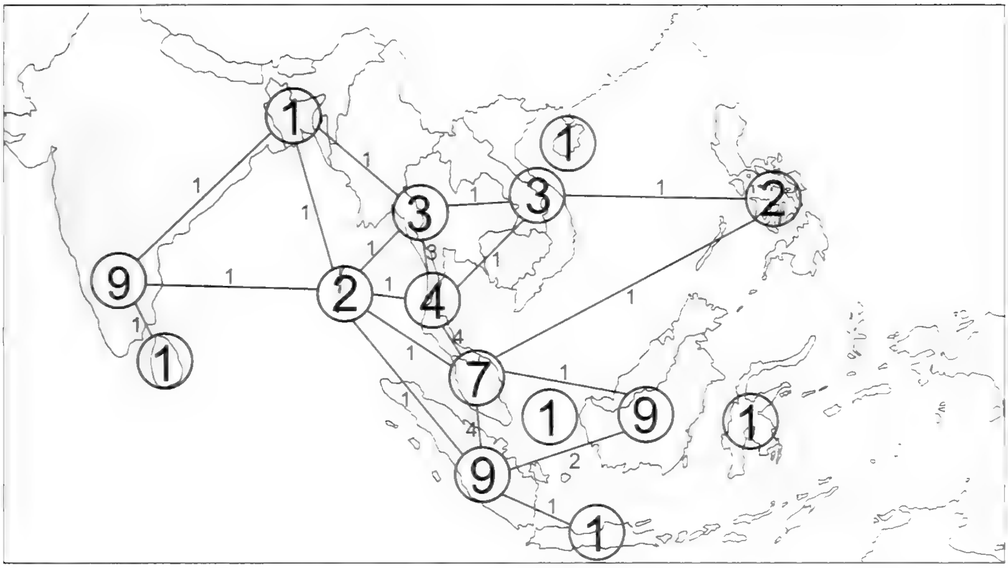

Fig. 3. Distribution and biodiversity similarity diagram for *Thottea* s.l. (Hou 1981) showing the number of species known for the respective biogeographic regions (in circles) and the number of species shared between them. Two diversity hotspots are observed: one in India (southern Western Ghats) and one in the Malesian region.

This species has only been reported from Borneo previously. This finding requires confirmation because *T. paucifida* and *T. tomentosa* can be confused due to superficial similarities. In addition, *T. paucifida* from the Andaman Islands is known only with fruits, whereas *T. paucifida* from Borneo was known only with flowers – which could exacerbate a comparison.

Thottea holds a potential key position with respect to growth form and woodiness evolution in the Piperales, being a potential link between the herbaceous Asaroideae and the woody Aristolochioideae. The genus *Aristolochia* is dominated by vines or lianas, but rarer shrub-like species are known. Close relationships between species having wide-ranging growth forms pose a number of questions concerning the processes by which highly different growth forms have evolved. Analysis of the developmental shifts in both primary and secondary development of the stem provides an implicit framework for identifying which structural and anatomical traits are adapted for life as herbs, shrub or lianas (Speck et al. 2003, Rowe & Speck 2005, Isnard et al. 2011, Wagner et al. in prep.). Ongoing studies are investigating to what extent heterochrony and relatively basic changes in developmental rate can radically influence the growth form and how specialisation and or canalisation of developmental traits, play a role in modifying the overall size and growth form of species within the Aristolochiaceae and Piperales.

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Permanent URL of the alignment and analyses data on TreeBASE:
http://purl.org/phylo/treebase/phylows/study/TB2:S11815

Appendix A. Field origin or Botanical Garden (BG) accession numbers, voucher information and GenBank accessions used in the present study. * For these specimens sequences of the *trnK* intron and *matK* gene were derived from earlier studies. The *trnK* 3' exon and *trnK-psbA* spacer were newly generated and submitted to genbank as an update of the original sequences.

Taxon	Field origin/ Botanical Garden accession no.	Voucher (herbarium)	Genebank accession no.	
			trnK intron, *matK* gene, *trnK-psbA* spacer	Source
Saruma Oliv.				
S. henryi Oliv.	BG Bonn, 02618	Borsch 3456 (BONN)	DQ532033	Wanke et al. 2007a & this study*
Asarum L.				
A. chingchengense C.Y.Cheng & C.S.Yang	BG Bonn, 02680	Neinhuis 90 (DR)	DQ882196	Wanke et al. 2007a & this study*
Aristolochia L.				
A. acuminata Lam.	BG Bonn, 17417	Wanke & Neinhuis 146 (DR)	DQ532063	Wanke et al. 2007a & this study*
A. acutifolia Duch.	Colombia, Meta	González-4176 (COL)	DQ532048	Wanke et al. 2006a & this study*
A. bracteolata Lam.	BG Bonn, 16714	Neinhuis 94 (DR)	DQ532059	Wanke et al. 2007a & this study*
A. clematitis L.	Croatia, Is Ilovik Asinello	Starmüller (KL)	DQ532060	Wanke et al. 2006a & this study*
A. gorgona M.A.Blanco	Heredia: Puerto Viejo de Sarapiquí, Costa Rica	Blanco 1752 (USJ)	DQ532051	Wanke et al. 2007a & this study*
A. holostylis F.González	BG Bonn, 02193	Neinhuis 116 (DR)	DQ532057	Wanke et al. 2007a & this study*
A. labiata Willd.	BG Bonn, 09867	Neinhuis 96 (DR)	DQ532055	Wanke et al. 2007a & this study*

A. lindneri A.Berger	Bolivia, San Jose de Chiquitos	Ibisch s.n. (DR)	DQ532047	Wanke et al. 2006a & this study*
A. manshuriensis Kom.	BG Bonn, 13085	Neinhuis 104 (DR)	DQ532040	Wanke et al. 2007a & this study*
A. micrantha Duch.	priv. coll. B.Westlund Texas, USA	Neinhuis 103 (DR)	DQ532046	Wanke et al. 2007a & this study*
A. panamensis Standl.	Panama, Panama	González-4018B (COL)	DQ532043	Wanke et al. 2006a & this study*
A. pistolochia L.	France, Cassis, Calenque d'En Veau	leg. Kreft, Wanke 37 (DR 25372)	DQ532062	Wanke et al. 2007a & this study*
A. promissa Mast.	BG Bonn, 13014	Neinhuis 118 (DR)	DQ532065	Wanke et al. 2007a & this study*
A. reticulata Nutt.	priv. coll. B.Westlund Texas, USA	Neinhuis 108 (DR)	DQ532037	Wanke et al. 2007a & this study*
A. rojasiana (Chodat & Hassl.) F.González	BG München s.n., Brazil, Mato Grosso	Wanke s.n. (DR)	DQ861635	Wanke et al. 2006a & this study*
A. rotunda L.	France, Corsica	Wanke 015 (DR)	DQ532061	Wanke et al. 2006a & this study*
A. serpentaria L.	priv. coll. B.Westlund Texas, USA	Neinhuis 112 (DR)	DQ532038	Wanke et al. 2007a & this study*
A. triactina Hook.f.	BG Bonn, 12767	Neinhuis 119 (DR)	DQ532066	Wanke et al. 2007a & this study*
Thottea Rottb.				
T. abrahamii M.Dan, P.J.Mathew, Unnithan & Pushp.	India, Kerala Trop. Bot. Garden	Pradeep s.n. (TBGT)	JN415669	this study
T. barberi (Gamble) Ding Hou	India, Kerala Trop. Bot. Garden	Pradeep s.n. (TBGT)	JN415675	this study
T. borneensis Valeton	Hort.Bogor XI.B.XIII.134, origin: Borneo	van Steenis 24294 (L 240977)	JN415668	this study
T. dalzellii (Hook.f.) Karthik. & Moorthy	India, Kerala Trop. Bot. Garden	Pradeep s.n. (TBGT)	JN415677	this study
T. dinghoui Swarupan.	India, Kerala Trop. Bot. Garden	Pradeep s.n. (TBGT)	JN415670	this study
T. duchartrei Sivar., A.Babu & Balach.	India, Kerala Trop. Bot. Garden	Pradeep s.n. (TBGT)	JN415678	this study

T. grandiflora Rottb.	Peninsular Malaysia, Selangor, Genting Sempah	B.C. Stone 6112 (PH 0961499)	JN415671	this study
T. idukkiana Pandur. & V.J.Nair	India, Kerala Trop. Bot. Garden	Pradeep s.n. (TBGT)	JN415680	this study
T. parviflora Ridl.	Thailand, Songkhla Province, Hat Yai	S.Chantanaorrapint 1265 (PSU)	JN415672	this study
T. penitilobata Ding Hou	Borneo, Brunei, Temburong, Batu Apoi Forest Reserve	Poulsen, A.D. 1 (AAU)	JN415673	this study
T. piperiformis (Griff.) Mabb.	Malaysia	Weber & Anthonysamy 870519-1/1 (WU)	DQ532036	Wanke et al. 2007a & this study*
T. ponmudiana Sivar.	India, Kerala Trop. Bot. Garden	Pradeep s.n. (TBGT)	JN415676	this study
T. siliquosa (Lamkey) Ding Hou	India, Kerala Trop. Bot. Garden	Pradeep s.n. (TBGT)	JN415679	this study
T. sivarajanii E.S.S.Kumar, A.E.S.Khan & Binu	India, Kerala Trop. Bot. Garden	Pradeep s.n. (TBGT)	JN415681	this study
Thottea sp.	BG Bonn, 09037, origin: India, Kerala, Thrissur District (Bogner 86-3421)	Neinhuis 121 (DR)	DQ532035	Wanke et al. 2007a & this study*
T. tomentosa (Blume) Ding Hou	Thailand, Phatthalung, Tha Mot	Larsen et al. 43958 (AAU)	JN415674	this study
Saururaceae Rich.				
Anemopsis californica (Nutt.) Hook. & Arn.	BG Bonn, 06422	Wanke 002 (DR)	DQ882198	Wanke et al. 2007a & this study*
Gymnotheca chinensis Decne.	BG Bonn, 17072	Wanke 004 (DR)	DQ882199	Wanke et al. 2007a & this study*
Saururus chinensis Hort. ex Loudon	BG Bonn, 00312	Wanke 001 (DR)	DQ212713	Wanke et al. 2006b & this study*

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Asian *Begonia*: out of Africa via the Himalayas?

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ABSTRACT. The large genus *Begonia* began to diverge in Africa during the Oligocene. The current hotspot of diversity for the genus in China and Southeast Asia must therefore be the result of an eastward dispersal or migration across the Asian continent. To investigate the role of the Himalayas as a mesic corridor facilitating this migration, we constructed a time-calibrated molecular phylogeny using ITS sequence data. Himalayan species of *Begonia* were found to fall into two groups. The first is an unresolved grade of tuberous, deciduous species of unknown geographic origin, with evidence of endemic radiations in the Himalayan region beginning c. 7.4 Ma, coinciding with the onset of the Asian monsoon. The second is a group of evergreen rhizomatous species with a probable origin in China, which immigrated to the Himalayan region c. 5.1 Ma, coinciding with an intensification of the monsoon. The hypothesis of the Himalayas being a mesic migration route during the colonisation of Asia is not refuted, but further data is needed.

Keywords. *Begonia*, biogeography, China, Himalayas, molecular phylogeny, southeast Asia

Introduction

The large genus *Begonia* has around 750 species in Asia, with the bulk occurring in Southeast Asia, and the Malesian region having c. 440 of these (Hughes 2008). Reconstructions of the phylogenetic history of *Begonia* show an early divergent African clade, with Asian and American species nested within an African grade (Plana et al. 2004, Forrest et al. 2005, Goodall-Copestake et al. 2010) and Asian (including Socotran) species supported as monophyletic (Goodall-Copestake et al. 2010, Thomas 2010). Given the initial diversification of *Begonia* in Africa in the Oligocene or late Eocene (Goodall-Copestake et al. 2009) and the monophyly of Asian species, there must have been a migration or dispersal of an ancestor eastwards from Africa which has speciated and led to the various diversity hotspots across Asia.

Molecular divergence age estimates indicate that the origins of Asian (including Socotran) *Begonia* date to 18–15 Ma (Thomas 2010) coinciding with the mid-Miocene climatic optimum, a warm phase which led to the expansion of tropical vegetation in Asia as far north as southern Japan and as far east as the northwest of the Indian subcontinent (Zachos et al. 2001, Morley 2007). However it would seem that a straightforward migration of *Begonia* across the Arabian peninsula to Asia is unlikely, given the dry conditions thought to have existed across much of southwest Asia and the Arabian peninsula at the time (Morley 2007). Hence a long distance dispersal event does not seem an unlikely hypothesis for the entry of an African ancestor into Asia, although this was possibly facilitated by the greater expanse of tropical climate during the mid-Miocene. *Begonia* from Sri Lanka, the Western Ghats and Socotra are at the western limit of the Asian *Begonia* clade (Fig. 1), and have been found to be early divergent lineages within a phylogeny of Asian species (Thomas 2010).

The Himalayas began to form during the initial collision of the Asian and Indian plates during the early Eocene c. 35 Ma (Ali & Aitchison 2008) and by the time of the arrival of *Begonia* in Asia c. 15 Ma, the High Himalayas were present (Amano & Taira 1992). Hence, depending on climate, there was potentially a significant area of montane habitat at the north of the Indian continent which could have provided a mesic link as a migration route eastwards towards the current *Begonia* diversity hotspots of Indo-China and Malesia (Fig. 1).

To investigate the role of the Himalayas as an easterly migration route during the colonisation of Asia, Himalayan species of *Begonia* were placed in a phylogeny to allow their interpretation in a geographical and temporal context. This paper builds on previous studies by considerably increasing the sampling of Himalayan species and coding the region as a distinct geographic unit in a biogeographic analysis. In particular, this paper addresses the following questions:

—Is there evidence for the Himalayas behaving as a link in an eastward migration of *Begonia*?

—How has paleo-climatic change and the Himalayan orogeny influenced the evolution of Nepalese *Begonia*?

Materials and methods

The molecular phylogenetic analysis was based on nuclear ribosomal internal transcribed spacer (ITS) sequences, obtained from Genbank and also *de novo* for this study (Appendix A) following the methods in Thomas (2010). Phylogenetic reconstruction, divergence times and ancestral area reconstruction were performed simultaneously using Bayesian inference as implemented in BEAST v1.6.1 (Drummond & Rambaut 2007), using 4×10^7 generations and sampling every 1000th generation. The sequence data was divided into three partitions, namely the two internal transcribed spacers (ITS1 and ITS2) and the 5.8s ribosomal gene. Models of sequence evolution for each nucleotide sequence partition were determined using jModelTest (Posada 2008). The divergence time for the split between African and Asian species was set as 17.8 Ma

Fig. 1. The distribution of *Begonia* in the Old World, highlighting the disjunction between the African and Asian floras, and the westward linear distribution along the Himalayas. Data from the GBIF data portal and Hughes & Pullan (2007).

(Thomas 2010), implemented as a normally distributed prior with a standard deviation of 3.4. Bayesian ancestral area reconstructions were performed using the continuous-time Markov chain (CTMC) model for discretized diffusion specified by Lemey et al. (2009), considering diffusion amongst 10 geographic areas defined as Africa, China, Himalaya, India, Indo-China, Philippines, Socotra, Sulawesi, Sunda Shelf and Taiwan. Maximum clade credibility consensus trees were made using TreeAnnotator v1.6.1 (Drummond & Rambaut 2007) with a burn-in of 25%, and visualised using FigTree v1.3.1 (Rambaut 2007).

The Bioclim parameter precipitation seasonality (Busby 1991) was extracted from the WorldClim database (Hijmans et al. 2005a) using DIVA-GIS (Hijmans et al. 2005b) and georeferenced herbarium specimen data from Hughes & Pullan (2007). It is calculated as the standard deviation of weekly precipitation estimates expressed as a percentage of the annual mean of those estimates. Scores for species with multiple localities were averaged.

Perennation organ type was scored from literature records and herbarium specimens available from Hughes & Pullan (2007).

Results

Sequence characterisation

The aligned sequences gave a dataset of 873 characters in length (ITS1 330 bases, 5.8s 148 bases, ITS2 395 bases). The bases at positions 492–499 and 505–525 were excluded from the analysis due to difficulty in reliably assigning positional homology. The remaining 845 bases were included in the analysis, of which 561 were variable and 433 (51%) were potentially informative (ITS1, 237 variable and 190 (58%) potentially informative; 5.8s, 31 variable and 11 (7%) potentially informative; ITS2, 294 variable and 232 (63%) potentially informative). All three regions were analysed under a GTR+G+I model (general time reversible model, gamma distributed rate variation, plus a proportion of invariable sites).

Phylogenetic analysis—geography and dating

The Asian + Socotra ingroup was supported as monophyletic with a posterior probability of 1 (Fig. 2). Relationships at the base of the tree were generally poorly supported, and hence inferences regarding timing and geography of cladogenesis on this part of the tree are not possible with confidence.

Clade A contains species from China, Indo China and Malesia, with several well supported sub-clades. One of these contains the Thai species *B. alicida* and *B. smithiae*, together with three species of *Begonia* sect. *Parvibegonia*. Two other supported subclades are highlighted (Fig. 2) concerning the large *Begonia* sect. *Petermannia* with a probable origin on the Sunda Shelf in the late Miocene followed by later diversification in Wallacea.

Himalayan species are present only in Clade B (Fig. 2), in both the 'Diploclinium grade' and the clade consisting of members of *Begonia* sect. *Platycentrum* and *Sphenanthera*, marked PLA-SPH in Fig. 2. The 'Diploclinium grade' has a largely unsupported topology at the base, but began diversifying sometime between 14.7 (±7.6) and 12.3 (±6.7) Ma in the mid-Miocene. Species from the Himalayan region in this grade are intermixed with species from China, Indo-China and Taiwan. Due to the unresolved backbone, the area of origin for this tuberous, seasonally adapted grade cannot be reconstructed. Supported subclades within the grade have areas of origin reconstructed as the Himalaya, Indo-China or China. One consists of the Taiwan endemic *B. ravenii* sister to two accessions of the Himalayan *B. dioica*; the geographic origin of this clade is equivocal, with the Himalayas having the highest posterior probability, though only of 0.37; it dates from 7.4 (±5.7) Ma. Another clade consists of four species from Thailand, probably representing speciation originating in that country (PP 0.84), dating from 8.1 (±5.2) Ma. A clade of species from Nepal, with *B. picta* appearing as sister to the remaining species, likely has a Himalayan origin (PP 0.90) dating 7.4 (±4.6) Ma. A clade with *Begonia puttii* (Thailand) and *B. labordei* (China) along with an unidentified species from China diverged 6.4 (±4.8) Ma in China (PP 0.82). The most highly nested subclade in the Diploclinium grade, sister to the PLA-SPH clade, contains three accessions of *Begonia* rubella from Nepal

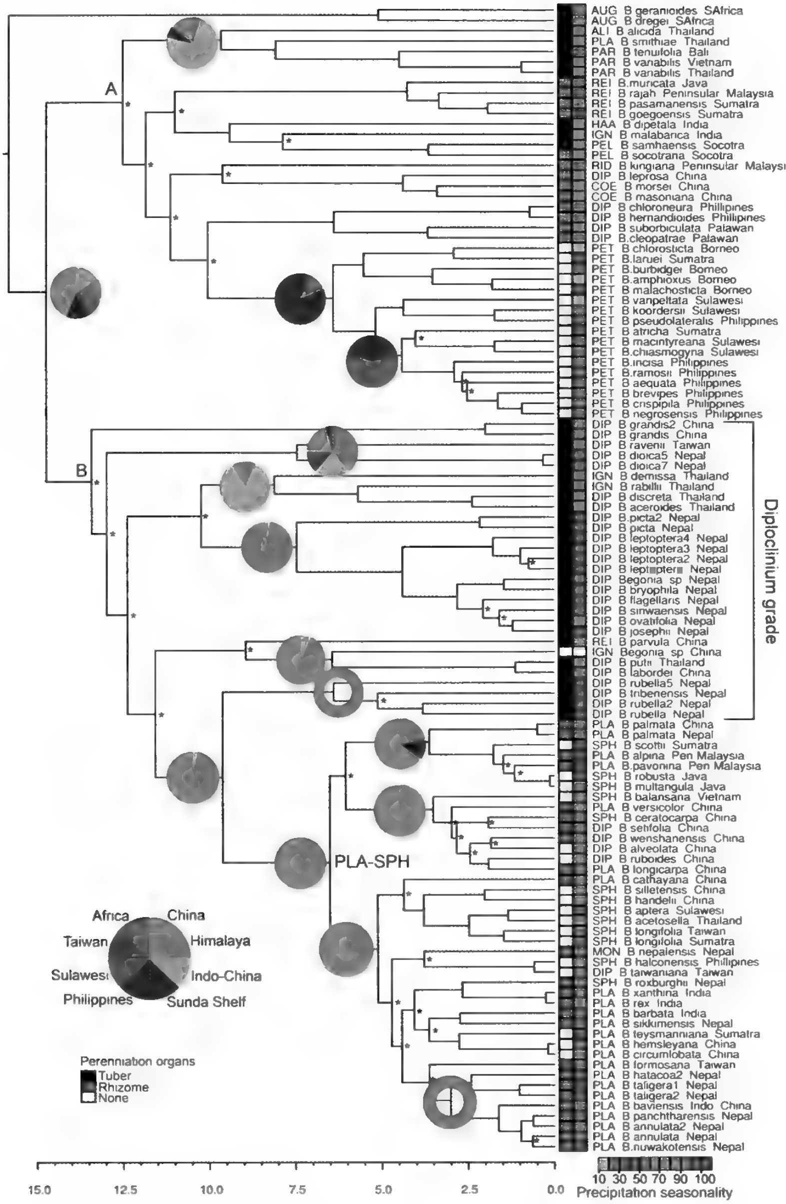

Fig. 2. Maximum clade credibility chronogram derived from an analysis of nuclear ribosomal ITS sequences using BEAST v1.6.1 (Drummond & Rambaut 2007). Asterisks denote clades with a posterior probability of less than 0.8; pie charts show Bayesian ancestral area reconstructions on supported nodes; lower scale denotes time in millions of years; the monochrome and coloured boxes at the branch tips show the perenniation organ type and precipitation seasonality respectively; missing data coded as white. Three-letter codes indicate the sections of *Begonia* (ALI, sect. *Alicida*; AUG, sect. *Augustia*; COE, sect. *Coelocentrum*; DIP, sect. *Diploclinium*; HAA, sect. *Haagea*; IGN, *ignota* (section unknown); MON, sect. *Monopteron*; PAR, sect. *Parvibegonia*; PET, sect. *Petermannia*; PLA, sect. *Platycentrum*; REI, sect. *Reichenheimea*; RID, sect. *Ridleyella*; SPH, sect. *Sphenanthera*).

and one of *B. tribenensis*, also from Nepal. This subclade probably has an origin in the Himalayas (PP 0.95) dated 6.4 (±4.3) Ma.

The origin of the PLA-SPH clade dates from 6.5 (±4) Ma and hence is considerably younger than the 'Diploclinium grade'. Himalayan species in the PLA-SPH clade are intermixed with species from China, Indo-China, the Sunda shelf, Taiwan, the Philippines and Sulawesi. The geographic area of origin for this clade is most probably China (PP 0.73). Three supported subclades within the PLA-SPH clade also have an area of origin optimised as China, with posterior probabilities of 0.65, 0.70 and 0.94. Only one subclade has a probable area of origin in the Himalaya (PP 0.99), dating from 3.0 (±2.3) Ma and with one dispersal into Indo-China. The overall picture for the PLA-SPH clade is of a fairly rapid diversification with its origins in China following loss of the tuberous habit, with dispersal to the Himalayan region and throughout Southeast Asia followed by localised speciation.

Phylogenetic analysis—perennation organs, precipitation and seasonality

All of the species in the 'Diploclinium grade' are tuberous and the vast majority are found in climates with a marked seasonality in rainfall (Fig. 2). They tend to die back and lose their leaves completely in the dry season. Species within the PLA-SPH clade either have a rhizome or no specialised perennation organs. The rainfall seasonality of the distributions of most of the species is much less marked than for those in the 'Diploclinium grade', and they do not lose their leaves during the dry season. Only one clade lacks perennation organs entirely, consisting of *Begonia* sect. *Petermannia* species distributed in the largely everwet Malesian region.

Discussion

Although support for the backbone of the tree was weak, the taxon composition of the two major clades, A and B, matches that of strongly supported clades found using chloroplast sequence data by Thomas (2010), with much greater sampling of Himalayan species in this study. In addition, the overall topology of clade B matches the results of Thomas (2010) with respect to a clade of *Begonia* sects. *Platycentrum* and *Sphenanthera* (PLA-SPH in Fig. 2) being nested within a grade consisting mainly of *Begonia* sect. *Diploclinium* species from the continent (labelled 'Diploclinium grade' in Fig. 2); also congruent is the Chinese species *B. grandis* being sister to the remaining taxa. The basal relationships in Clade A are unsupported, but the supported subclades within Clade A are similar to those found by Thomas (2010), and generally correspond to species of a single section or geographic region. This congruence gives some confidence in the tree topology, despite the disappointing levels of support.

The Himalayas as a link in an eastward Begonia migration

If the Himalayas acted as a migration corridor in the early evolution of Asian *Begonia*, we would expect to see other species in Asia nested within a Himalayan grade in the phylogeny. Due to the unsupported nodes at the base of the clade containing all the

Himalayan species, evidence for this is equivocal. Of the two major sections in the Himalayan *Begonia* flora (*Begonia* sects. *Diploclinium* and *Platycentrum*), *Begonia* sect. *Diploclinium* has the oldest lineages which date to between 14.7 (±7.6) and 12.3 (±6.7) Ma and accounts for nearly 60% of the species in Nepal. Some subclades in this group do show a likely Himalayan origin, but the supported nodes are dated in the late Miocene at c. 7.5 Ma and so post-date the early divergence of the section. Further work on other gene regions is needed to resolve the relationships in the 'Diploclinium grade'. The hypothesis of basally branching Himalayan lineages in *Begonia* sect. *Diploclinium* is not refuted by our results. However, the fact that the Chinese species *B. grandis* is possibly sister to the rest of the 'Diploclinium grade' is tantalising and raises the possibility of China being an ancestral area for this group.

The other major section, *Begonia* sect. *Platycentrum*, accounts for 35% of Nepalese species. The species are all included in the PLA-SPH clade with an origin in the late Miocene–early Pliocene. There is no evidence for the Himalayan species in *Begonia* sect. *Platycentrum* being relicts from an eastward migration early in the evolution of Asian *Begonia*, in fact the emerging picture is the exact opposite. This clade has a probable Chinese origin, and represents an entry of the genus into the Himalayan region separate from those in the 'Diploclinium grade'. The Himalayan species are largely highly nested within this clade and there is evidence for more than one migration into the Himalayan region, including a very recent one in the late Pliocene–early Pleistocene (bottom of Fig 2; clade from *B. hatacoa* to *B. nuwakotensis*).

Other major clades containing the bulk of species diversity in Southeast Asia (*Begonia* sect. *Petermannia* from Malesia; *Begonia* sect. *Diploclinium* from the Philippines; *Begonia* sect. *Reichenheimia* from the Sunda shelf) remain unsupported in Clade A. Our results do not show any affinity of these clades with Himalayan taxa, and the origin of these large radiations remains enigmatic.

Paleo-climatic change, Himalayan orogeny and evolution of Nepalese Begonia

It is possible to highlight two main events in the evolution of the Himalayan *Begonia* flora—the mid- to late Miocene diversification of the tuberous, seasonally adapted 'Diploclinium grade' and the late Miocene–Pliocene immigration and diversification of the rhizomatous and evergreen PLA-SPH clade.

The early diversification of tuberous clades with a likely origin in the Himalayas can be dated to between 6.4 (±4.8) and 7.4 (±4.6) Ma. This coincides with the development of the Asian monsoon 7.4 Ma (Copeland 1997), due to the Tibetan plateau having reached sufficient altitudes to affect a major re-organisation of atmospheric circulation over the Asian continent (Zheng et al. 2004). The tuberous species would be well adapted to this seasonal monsoon climate, with concentrated periods of intense rainfall interspersed with significant dry seasons. These species are deciduous, and their flowering periods are strongly constrained to the three months after the onset of the monsoon (Rajbhandary et al. 2010). The subsequently formed dry dehiscent capsular fruits are then able to disperse their seeds either passively or through wind assistance during the following dry season.

The immigration of members of the PLA-SPH clade into the Himalayan region began 5.1 (±3.2) Ma, with an endemic radiation starting 3.0 (±2.1) Ma and continuing throughout the Pleistocene. The immigration coincides with a further intensification of the Asian monsoon around 5 to 3.6 Ma, possibly linked to a further surge in the uplift of the Himalayas and the Tibetan plateau (Zheng et al. 2004, Zhisheng et al. 2001) and changes in ocean currents in the Indo-Pacific region (Srinivasan & Sinha 2000). The evolution of an evergreen, rhizomatous habit in this clade suggests adaptations to wetter conditions, but the details of how the Pliocene monsoon intensification affected total and seasonal rainfall in the Chinese (presumably SW China) region where the PLA-SPH clade originated are unknown. The Himalayan species in this clade currently occur in areas with similar rainfall seasonality to the tuberous species, but occupy different micro habitats where water is more constantly available; their flowering is not strongly constrained by the monsoon (Rajbhandary et al. 2010). They have fruits which are adapted to rain-splash seed dispersal, and hence depend on either rainfall or drips and splashes from waterfalls to disperse. Our results are congruent with those of Tebbitt et al. (2006), who suggested that members of *Begonia* sect. *Platycentrum*, which have fruit morphologies indicative of rain dispersal, evolved from wind-dispersed Asian taxa following the colonisation of wetter habitats.

Of the two groups of *Begonia* in the Himalayas, seasonally deciduous and evergreen, only the former could possibly be relicts of an eastward migration. However, due to the unresolved relationships of clades within this group, their origins remain unknown. The evergreen species represent a re-entry to the Himalayan region, most likely from China, and have speciated in response to further tectonic uplift and Pliocene–Pleistocene climatic cycles and changes in the monsoon intensity. These factors are also likely to have strongly influenced the recent diversification of other elements of the Himalayan flora. Further phylogenetic studies of Himalayan plants will reveal the relative contribution of relict clades and recent speciation to the considerable plant diversity in the region.

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Appendix A. List of the Genbank accession numbers of the DNA sequences used in the phylogenetic analysis.

B. aceroides, HQ729023; *B. acetosella*, AY048976; *B. aequata*, AF48514; *B. alicida*, HQ729022; *B. alpina*, AY753717; *B. alveolata*, AY048977; *B. amphioxus*, AF485150; *B. annulata*, HQ729060; *B. annulata2*, HQ729059; *B. aptera*, AF48510; *B. atricha*, HQ729047; *B. balansana*, AF485091; *B. barbata*, AF485095; *B. baviensis*, AF485087; *B. brevipes*, HQ729048; *B. bryophila*, HQ729030; *B. burbidgei*, HQ729049; *B. cathayana*, AF280106; *B. ceratocarpa*, AY048978; *B. chiasmogyna*, HQ729050; *B. chloroneura*, AF485134 ; *B. chlorostricta*, AF485153; *B. circumlobata*, AY753721; *B. cleopatrae*, AF485133; *B. crispipila*, HQ729051; *B. demissa*, HQ729026; *B. dioica1*, HQ729039; *B. dioica2*, HQ729038; *B. dipetala*, AF485142; *B. discreta*, HQ729024; *B. dregei*, AY429336; *B. flagellaris*, HQ729031; *B.formosana*, AF485119; *B. geranioides*, AF469120; *B. goegoensis*, AF485138; *B. grandis*, AF485089; *B. grandis2*, AF485088; *B. halconensis*, AF485106; *B. handelii*, AY048982; *B. hatacoa2*, AF485111; *B. hemsleyana*, AF485099; *B.hernandioides*, AF485135; *B. hyatae*, AJ287262; *B. incisa*, AF485148; *B. josephii2*, HQ729037; *B. kingiana*, AF485139; *B. koordersii*, HQ729052; *B. labordei*, AF485122; *B. laruei*, HQ729058; *B. leprosa*, AY753722; *B. leptoptera*, HQ729036; *B. leptoptera2*, HQ729033; *B. leptoptera3*, HQ729034; *B. leptoptera4*, HQ729035; *B. longicarpa*, AF485109; *B. longifolia*, AF485105; *B. macintyreana*, HQ729054; *B. malabarica*, AF468141; *B. malachosticta*, AF485156; *B. masoniana*, AF485123; *B. morsei*, AF485130; *B. multangula*, AY753724; *B. muricata*, AY753725; *B. negrosensis*, HQ729055; *B. nepalensis*, AY753726; *B. nuwakotensis*, HQ729061; *B. ovatifolia*, HQ729032; *B. palmata*, AF485113.1; *B. palmata*, AF485115.1; *B. panchtharensis*, HQ729062; *B. parvula*, GU176066; *B. pasamanensis*, HQ729070; *B. pavonina*, AY753727; *B. picta*, HQ729042; *B. picta2*, HQ729041; *B. pseudolateralis*, HQ729053; *B. putii*, HQ729025; *B. rabillii*, HQ729027; *B. rajah*, AF485136; *B. ramosii*, HQ729057; *B. ravenii*, HQ729040; *B. rex*, AY753728; *B. robusta*, AY753729; *B. roxburghii*, AF485092; *B. rubella*, AF485112; *B. rubella2*, HQ729043; *B. rubella5*, HQ729044; *B. ruboides*, AY048987; *B. samhaensis*, AF469122; *B. scottii*, HQ729063; *B. setifolia*, AY048990; *B. sikkimensis*, HQ729064; *B. silletensis*, AF485094; *B. sinwaensis*, HQ729029; *B. smithiae*, HQ729065; *B. socotrana*, AF469121; *B. suborbiculata*, HQ729069; *B. taiwaniana*, AY753731; *B. taligera1*, HQ729066; *B. taligera2*, HQ729067; *B. tenuifolia*, HQ873478; *B. teysmanniana*, HQ729068; *B. tribenensis*, HQ729045; *B. variabilis*, AY753732; *B. variabilis*, HQ729046; *B. varipeltata*, HQ729056; *B. versicolor*, AF485090; *B. wenshanensis*, AY048974; *B. xanthina*, AY753733; *Begonia* sp. (China), GU176063; *Begonia* sp. (Nepal), HQ729028.

Distribution patterns in Malesian *Callicarpa* (Lamiaceae)

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ABSTRACT. A revision of the 55 species of *Callicarpa* L. (Lamiaceae) in Malesia is almost complete. There appear to be two major centres of diversity, in terms of species numbers: Borneo has 23 (44%) of the species (Bramley 2009), with 19 (83%) endemic; the Philippines has 26 (50%) of the species of which 16 (61%) are endemic (Bramley, in press, a). *Callicarpa* species have an extensive variation in distribution patterns; this paper focuses on the Pan-Malesian species, and the species of Borneo and the Philippines, the two islands island groups that are the centre of *Callicarpa* species diversity. Fifteen of the 19 *Callicarpa* species endemic to Borneo belong to the 'Geunsia' group, an informal group used here to recognise *Callicarpa pentandra* and its relatives. The Geunsia group appears to be restricted to Malesia, and is only represented by *C. pentandra* outside of Borneo, the Philippines and Sulawesi. The 16 *Callicarpa* species endemic to the islands of the Philippines represent a number of different informal morphology-based groups containing species from other areas of Malesia, China or Indo-China, or, they do not appear to belong to any particular group.

Keywords. Borneo, *Callicarpa*, centres of diversity, distribution, endemism, Malesia, Philippines

Introduction

A revision of *Callicarpa* L. (Lamiaceae) in Malesia is almost complete. It will form part of an addition and update (Bramley et al., in prep.) to Keng's Flora Malesiana account of the Labiatae (1968). *Callicarpa* and a number of other genera in the Verbenaceae, including *Vitex* L., *Premna* L. and *Clerodendrum* L., have been transferred to the Lamiaceae (Cantino et al. 1992, Harley et al. 2004) based on morphological characters, especially cymose versus racemose inflorescence, and a tubular and bilabiate versus salverform corolla; these characters are supported by embryological and pollen characters, and corroborated by analyses of cpDNA sequences (e.g., Olmstead et al. 2001).

There are about 140 species of *Callicarpa*, occurring in both temperate and tropical regions, although this number may be inflated due to currently unrecognised synonyms. In the New World there are 33 species recognised, particularly in the Caribbean Islands (24 species currently recognised on Cuba). The genus is more species rich in the Old World, with one species in Madagascar, c. 48 species in Temperate Asia, particularly China, 55 in Malesia, seven in Australia, and three in the Pacific. In general, the common and well-known species are shrubs or small trees found in disturbed areas such as secondary forest or roadsides, but a number of lesser known species inhabit primary forest only. Due to their use in horticulture, *Callicarpa americana* L., *C. japonica* Thunb., *C. dichotoma* (Lour.) K.Koch and *C. bodinieri* var. *giraldii* (Hesse ex Rehder) Rehder are widespread.

The 55 Malesian species of *Callicarpa* are unevenly distributed across the region (Fig. 1). Only two species have a pan-Malesian distribution, being present on all islands and groups of islands: *Callicarpa longifolia* Lam. and *Callicarpa pentandra* Roxb. There appear to be two major centres of diversity, in terms of species numbers: Borneo has 23 (44%) of the species (Bramley 2009), with 19 (83%) endemic; the Philippines has 26 (50%) of the species of which 16 (61%) are endemic (Bramley, in press, a). Less species rich is the Thai-Malay Peninsula with a total of eight species, of which one is endemic. Sumatra and Java share seven of these species, neither island has any endemic species. Sulawesi has six species currently recognised, one of which is endemic, and three further endemic species are being described as new to science (Bramley, in press, b). The Lesser Sunda Islands have only three species, and the Moluccas four species, none of which are endemic; New Guinea is home to seven species.

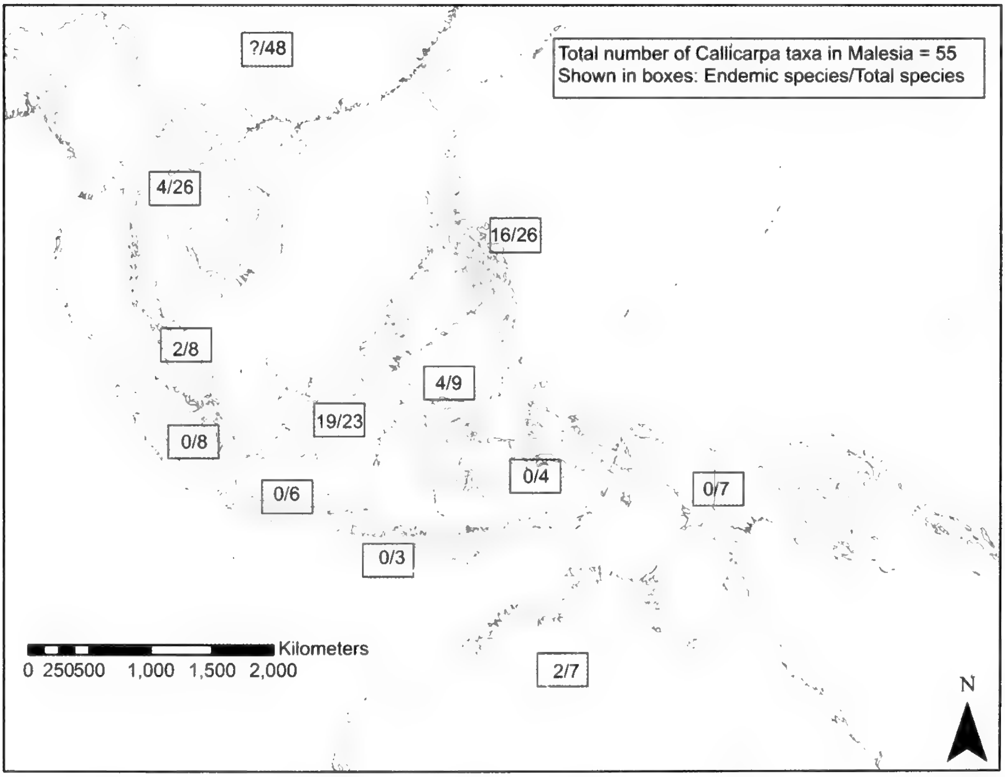

Fig. 1. Map showing the numbers of *Callicarpa* species in each island / island group across the Malesian region. In each box the number to the left represents the number of *Callicarpa* species endemic to that area; the number to the right is the total number of *Callicarpa* species found in that area.

Understanding why some species are widespread and others endemic to particular areas is becoming especially important in this era of habitat destruction and climate change. If we are to meet the targets set out by the Global Strategy for Plant Conservation, there must be an increase in the rate of production of species level conservation assessments (Nic Lughadha et al. 2005). Now that the taxonomy of Malesian *Callicarpa* has been studied, and species delimitation clarified, it is possible to map the distribution of each species based on data from Herbarium specimens. Not only does this allow preliminary conservation assessments to be undertaken, it encourages thought on what morphological characters might facilitate species to inhabit a particular environment, or enable a species to be widespread and apparently successful in more varied environments (Graham et al. 2004). Thoughts on the latter may be useful in any attempts to restore vegetation in disturbed areas.

Malesia has a rich geological history and many studies have focused on distributions of plant families and genera within it, with less of a focus on species. Divisions between areas have been postulated (e.g., Wallace's line), and frontiers marked between different floristic regions (e.g. van Steenis 1950; van Welzen & Slik 2009). By examining the distributions of Malesian *Callicarpa* species, I wish to determine whether there are any common and easy to define patterns that represent groups linked by morphological characters and geography. In this way I might be able to suggest key characters that enable survival or speciation in particular environments. I will make brief comparisons between patterns within *Callicarpa* and other Lamiaceae genera in Malesia. There will be no formal analysis: following the rationale of Baker et al. (1998), this paper is a descriptive precursor to any future analytical biogeographical project.

Materials and methods

Label information from specimens of Malesian *Callicarpa* from BM, BO, C, E, GH, K, KEP, L, NY, SING, SNP, US (abbreviations following Index Herbariorum, Thiers [continuously updated]) was captured in a Microsoft Access database; collecting localities were georeferenced if latitudes and longitudes were not already provided on the specimen label. The online gazetteer GEOnet Names Server (http://earth-info.nga.mil/gns/html/index.html) was used as a source for place names as well as the Google search engine (www.google.com) and printed maps.

Specimen data was exported from Access into ArcView 3.3, and each species distribution plotted using the Conservation Assessment Tools (CATS) extension developed at RBG Kew (Moat 2007).

Distribution patterns, species groups and phytogeographical relationships

Callicarpa species show extensive variation in distribution patterns and each pattern is not described in detail here. Instead I focus on three groups of particular interest:

the Pan-Malesian species, because only this distribution is surprisingly rare, and the Bornean and Philippine species, because these two islands / island groups are the centres of diversity. For a quick reference to the distribution of individual taxa, see Table 1.

Table 1. Malesian *Callicarpa* species and the areas in which they occur (excluding three new species from Sulawesi, Bramley, in press, b). (Left to right) THA = Thailand; MLY = Peninsular Malaysia; SUM = Sumatra; BOR= Borneo; PHI = Philippines; JAW = Java; SUL = Sulawesi; LSI = Lesser Sunda Islands; MOL = Moluccas; NWG = New Guinea; AUS = Australia. Other Areas: C = China, SC = South China, PAC = Pacific, T = Taiwan, V = Vietnam.

Callicarpa species	THA	MLY	SUM	BOR	PHI	JAW	SUL	LSI	MOL	NWG	AUS	Other areas
albidotomentella					x							
angusta					x							?V
angustifolia	x	x	x									V
anomala				x								
apoensis					x							
arborea	x	x	x		x	x						
argentii				x								
badipilosa				x								
barbata				x								
basilanensis					x							
bicolor					x		x			x		PAC
candicans	x	x	x	x		x		x	x		x	C
caudata					x		x		x	x		
cinnamoea							x					
clemensorum				x								
coriacea				x								
denticulata					x							
dolichophylla					x							T, C
endertii				x								
erioclona				x	x	x	x	x	x	x		V
fasciculiflora					x							
flavida					x							
fulvohirsuta				x								
furfuracea	x	x	x			x						
glabrifolia				x								
havilandii				x								
hispida				x								
involucrata				x								
kinabaluensis				x								
longifolia	x	x	x	x	x	x	x	x	x	x	x	

longipetiolata					x						
magnifolia					x						
maingayii	x	x									
micrantha					x						
pachyclada					x						
paloensis					x						
pedunculata					x			x	x	x	SC, T
pentandra	x	x	x	x	x	x	x	x	x	x	
platyphylla					x						
plumosa					x						
ramiflora					x						
rubella	x	x	x								V, C
saccata				x							
scandens				x							
stapfii				x							
subaequalis				x							
subalbida					x						
subglandulosa					x						
subintegra					x						
superposita				x							
surigaensis					x						
teneriflora				x							

Pan-Malesian species

Only two species have a distribution that includes all areas within Malesia: *Callicarpa pentandra* Roxb., and *C. longifolia* Lam. (Fig. 2).

Callicarpa pentandra is a small tree commonly found along roadsides and in secondary forest. Its distribution extends to Thailand in the North and to New Britain in the East, it is possibly present in the Solomon Islands but the material from the area has not yet been examined closely. *Callicarpa pentandra* is distinct from typical members of the genus because it has pentamerous rather than 4-merous flowers, larger oblong rather than elliptical anthers and a fruit with five locules each with two ovules giving a total of ten seeds, rather than the typical four (Fig. 3). As discussed in Bramley (2009) it formed part of the genus *Geunsia* Blume (now included in *Callicarpa*), on the basis of the characters listed above, and others. Further reference to this 'Geunsia' group will be made in a later section on the Borneo Endemics. *Callicarpa pentandra* has been noted as a pioneer species (Tsai 1991); its bright red fruit is likely to be bird-dispersed, and given that it has more than double the typical number of seeds than other member of the genus, it is likely to have an advantage in numbers of seed in the soil seed bank.

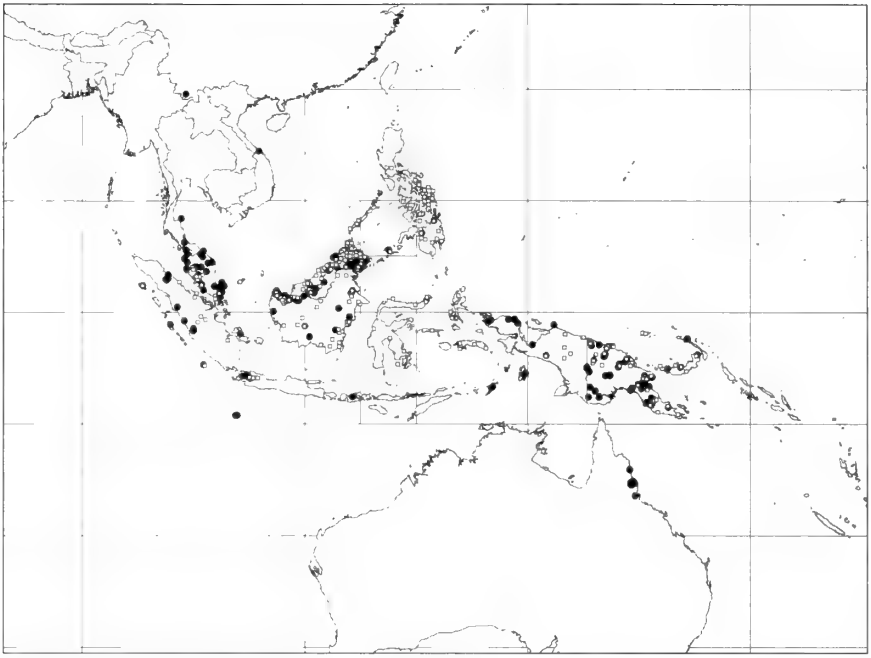

Fig. 2. Distribution of *Callicarpa pentandra* (grey squares) and *C. longifolia* (black circles).

Callicarpa longifolia extends further south than *C. pentandra*, to Australia. Its morphology is more typical for the genus; it has small 4-merous flowers, it is a shrub rather than a tree, and has only 4 locules per ovary, with 1 ovule per locule. The fruit however is white, rather than the more typical purple, and very fleshy—although this is difficult to see in dry material (Fig. 3). In this case I assume its success in secondary habitats is due to the attractiveness of the juicy fruit which is readily dispersed by birds or rodents such as treeshrews (Fletcher 1938, Snow 1981).

Borneo endemics

There are 19 *Callicarpa* species endemic to Borneo. Four of these endemic species have the 4-merous flowers and four ovules that are typical for the genus. The remaining fifteen species belong to the 'Geunsia' group, an informal group that I am using to recognise *Callicarpa pentandra* and its relatives. Along with C. *pentandra*, they have features once recognised under the genus *Geunsia* Blume (see Bramley 2009: 417). Unlike C. *pentandra*, they typically have 4-merous flowers but still have two rather than one ovule per locule than typical for the genus. Unusually, *C. hispida* (Moldenke) Bramley can have up to 7-merous flowers, with a total of 14 ovules (2 in each of its seven locules) (Fig. 4). Some of these species are widespread across Borneo (*C. havilandii* (King & Gamble) H.J.Lam), others are only known from much smaller areas (e.g., *C. argentii* Bramley; *C. anomala* (Ridl.) B.L.Burtt; *C. subaequalis* Bramley). All of these species have a fruit that ripens red which is larger than typical for *Callicarpa*, presumably because of the larger number of developing seeds (Fig. 3). In addition, a number of the species have a dense ferruginous indumentum of various different hair

Fig. 3. *Callicarpa longifolia*: **A.** Flowering branch. **B.** Fruits. *Callicarpa pentandra*: **C.** Flowering and fruiting branch. **D.** Fruiting branch. **E.** Habit.

types (see Bramley 2009). All tend to be found in areas of primary forest, often with some degree of disturbance.

Of additional interest are *C. kinabaluensis* Bakh. & Heine and *C. clemensorum* Moldenke, found at high altitude (1600–2500 m) on the peaks surrounding Mount Kinabalu: they are both extremely hairy and have inflorescences made up of almost globose cymes, perhaps an adaptation to their environment.

Philippines endemics

The 16 *Callicarpa* species endemic to the islands of the Philippines represent a number of different informal morphology-based groups containing species from other

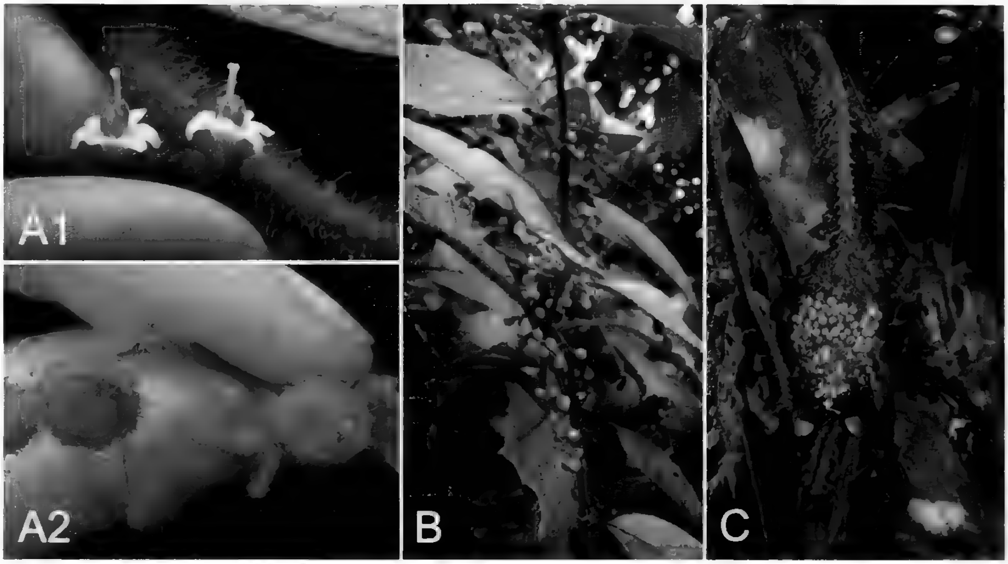

Fig. 4. Examples of Geunsia group species from Borneo. **A.** *Callicarpa hispida* (Moldenke) Bramley: A1, 7-merous flowers; A2, fruits cut open to reveal 14 ovules. **B.** *Callicarpa havilandii* (King & Gamble) H.J.Lam. **C.** *Callicarpa involucrata* Merr.

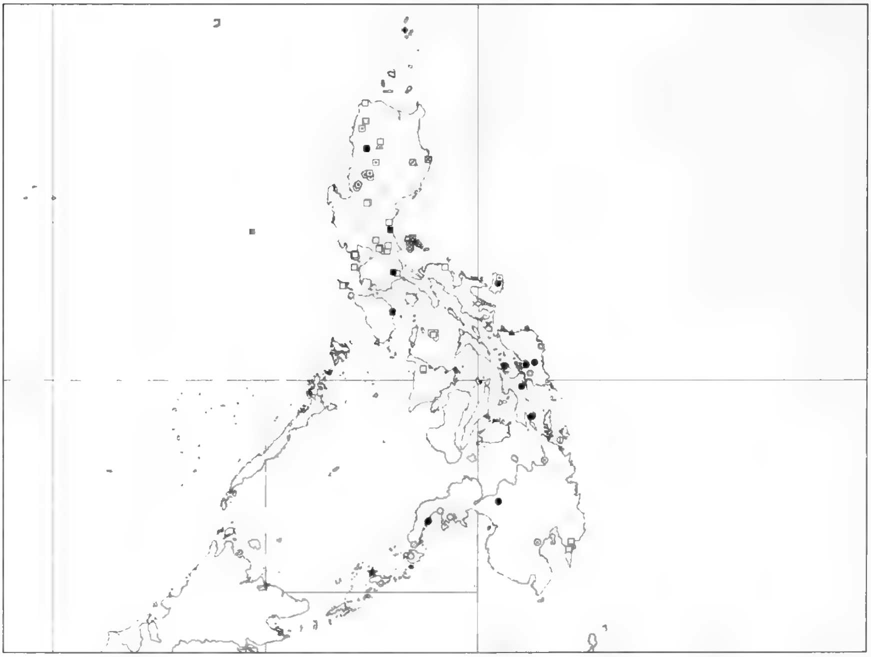

Fig. 5. Distributions of species endemic to the Philippines. Most species have narrow distributions (each species is signified by a different symbol), the exception being *C. micrantha* (grey squares). The Geunsia group of species are restricted to the southern islands (circular symbols).

areas of Malesian, China or Indo-China, to be detailed in the forthcoming revision of Philippine Callicarpa (Bramley, in press, a), or, they do not appear to belong to any particular group.

Most of the endemic species appear to have narrow ranges (Fig. 5). Only *C. micrantha* Vidal occurs throughout the Philippine islands. It is morphologically similar, through its delicate inflorescence, to the widespread *C. japonica*, native to China and Japan. There is a general divide between the Luzon and the Mindanao island groups. Most species present in the Luzon area are not present further south than the northern tip of Samar, with the exception of *C. micrantha*. The species endemic to the Mindanao islands are members of the Geunsia group (Basilan and Mindanao—*C. basilanensis* Merr., *C. flavida* Elmer, *C. ramiflora* Merr., *C. surigaensis* Merr.; Samar—*C. ramiflora*), with the exception of *C. apoensis* Elmer (endemic to Mount Apo). The furthest north the Geunsia group extends is Morong, in Rizal Province, Luzon (14°31'N 121°14'E; *Vidal 3430*), represented by the widespread C. *pentandra*. The Geunsia group appears to be restricted to Malesia, and is only represented by *C. pentandra* outside of Borneo, the Philippines and Sulawesi.

The species that occur in the Philippines as well as other areas appear to have eastern Malesian distributions, sometimes extending to Indo-China, but they do not occur in Sundaland (Fig. 6). For example, *C. pedunculata* R.Br. is a widespread species that does not occur further west than the Philippines. Perhaps this can be explained by a habitat requirement for seasonality: as described by van Steenis (1979), the western side of the Philippines, as well as parts of Sulawesi and New Guinea, are considered

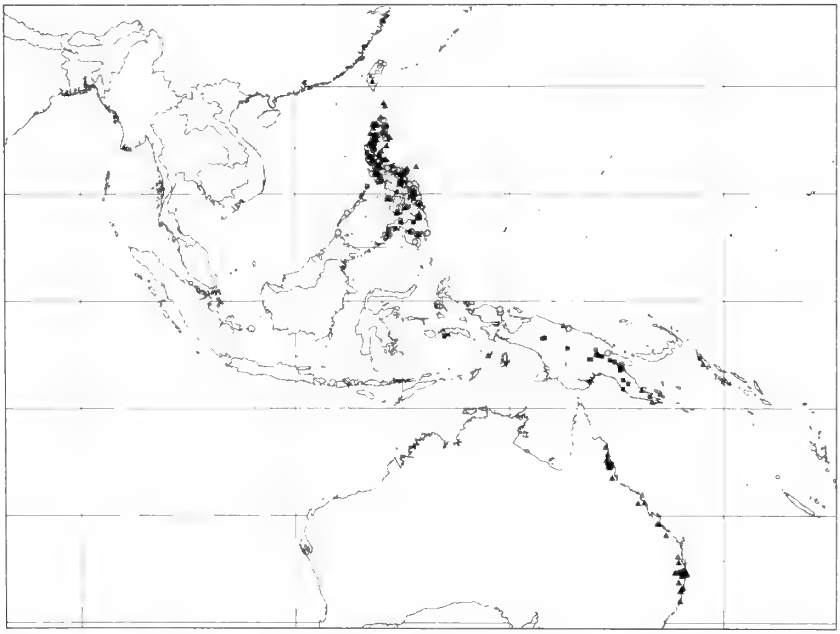

Fig. 6. Examples of *Callicarpa* species with Eastern Malesian distributions: *C. pedunculata* R.Br. (triangles), *C. erioclona* Schauer (grey circles), *C. caudata* Maxim. (black squares), *C. dolichophylla* Merr. (grey squares).

seasonal or monsoon areas. Likewise, *C. erioclona* Schauer is found from Vietnam, through the Philippines, on Java, in Sulawesi and New Guinea and has been recorded once from each of Kudat and Banggi Islands off Sabah. Lack of spread to the west is again perhaps likely to be a result of a preference for a degree of seasonality.

Callicarpa in comparison to other Lamiaceae genera

Callicarpa can be described as a Sunda Shelf and Wallacea oriented genus, with little presence in the Sahul Shelf (regions as defined by van Welzen & Slik (2009)). *Premna* (14 spp.; de Kok, in press), *Vitex* (16 spp., de Kok (2008)), *Teijsmanniodendron* (23 spp., de Kok et al. (2009)) are other Lamiaceae genera with similar distributions but are much smaller than *Callicarpa* in terms of species numbers in Malesia. Only *Clerodendrum* (65–70 spp., J. Wearn, pers. comm.) surpasses *Callicarpa* in terms of species numbers. *Premna* and *Vitex* have been revised by Rogier de Kok (2007, 2008; submitted), and *Clerodendrum* is under revision (Wearn & Mabberley, in prep.).

In terms of the numbers of species endemic to islands or island groups, *Callicarpa* is unusual. For example, there are only seven out of 22 species of *Clerodendrum* endemic to the Philippines (J. Wearn, pers. comm.). On Borneo, the only comparable genus may be *Teijsmanniodendron*: all of its 23 species occur on the island, and 11 of these are endemic (de Kok et al. 2009).

A team of volunteers have begun to database the Malesian Lamiaceae collections at K: once all specimens have been georeferenced and distribution maps completed for each genus, the baseline data for a comparative study of generic distributions will be provided. A particularly interesting question is why some genera appear to have radiated on the island of Borneo, the Geunsia group of *Callicarpa* especially. In addition, van Welzen & Slik (2010) recently reported that Lamiaceae *sensu* Lindley, treated for the Flora Malesiana by Keng (1968), is an example of a family with relatively high numbers of species (more than expected) in Wallacea. This makes for an interesting comparison with the woody genera transferred from the Verbenaceae discussed here.

Questions to be addressed in future research

This descriptive paper aims to act as a precursor to any future phylogenetic or biogeographic analyses. To be able to test whether the morphological groups discussed reflect evolutionary relationships between species, we need to elucidate the relationships between species (to date I only have a limited phylogeny). Furthermore, to understand the distribution of *Callicarpa* more generally, and to make comparisons with other Lamiaceae genera, I need to understand the position of *Callicarpa* within the Lamiaceae, a project also requiring phylogenetic work. In some preliminary analyses it has appeared close to the Australian subfamily Prostantheroideae Luerssen (Bramley, unpubl.). Indeed *Callicarpa* does share, at least superficially, some characters with the tribe Chlorantheae Benth. & Hook.: actinomorphic flowers, branched hairs, variable number of stamens. There is currently no solid evidence to support this position but it would be interesting to pursue this line of investigation, and also the developmental basis of the actinomorphic flower structure, rare within the Lamiaceae as a whole.

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How did Magnolias (Magnoliaceae: Magnolioideae) reach Tropical Asia?

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ABSTRACT. Extant magnolias (Magnoliaceae, Magnolioideae) have a classic disjunct distribution in southeast Asia and in the Americas between Canada and Brazil. Molecular analyses reveal that several North American species are basal forms suggesting that magnolias originated in North America, as indicated by their fossil record. We recognise four elements in their evolution: (1) Ancestral magnolias originated in the Late Cretaceous of North America in high mid-latitudes (45°–60°N) at low altitudes in a greenhouse climate. (2) During the exceptionally warm climate of the Eocene, magnolias spread eastwards, via the Disko Island and Thulean isthmuses, first to Europe, and then across Asia, still at low altitudes and high mid-latitudes. (3) With mid-Cenozoic global cooling, they shifted to lower mid-latitudes (30°–45°N), becoming extinct in Europe (*Yulania* was still present less than 2 mya.) and southern Siberia, dividing a once continuous distribution into two, centered in eastern Asia and in North America. (4) In the late Cenozoic, as ice-house conditions developed, magnolias migrated southward from both centres into moist warm temperate upland sites in the newly uplifted mountain ranges of South and Central America, southeast Asia, and the High Archipelago, where they diversified. Thus the late Cenozoic evolution of magnolias is characterised by impoverishment of northern, and diversification of southern species, the latter being driven by a combination of high relief and climate oscillations, and neither of the present centres of diversity is the centre of origin. Magnolioideae appear to consist of only the genus *Magnolia*.

Keywords. Magnoliaceae, Magnolia, fossils, DNA distribution, paleoclimate

Introduction

Understanding the present distribution (Fig. 1) and fossil occurrence (Fig. 2) of an ancient land-based group such as magnolias (subfamily Magnolioideae in the family Magnoliaceae) has to be done in relation to the historical disposition of land and global climate. For his Ph.D. (1956–59) Neil Opdyke studied the relationships between paleomagnetically determined latitudes and paleoclimates as inferred from temperature-sensitive deposits and from wind directions in eolian sandstones [Opdyke 1961a,b]. By placing such geological deposits at their original latitude, he was able to discuss possible past changes in climatic zones and in the positions of continents. Being able to do so is the key to unravelling the origin and paleogeographical dispersal of plant groups and individual species, in a way not available to earlier phytogeographers.

The genus *Magnolia* was described by Linnaeus in 1753 from material collected in what were then colonies of British North America. The type species is *Magnolia*

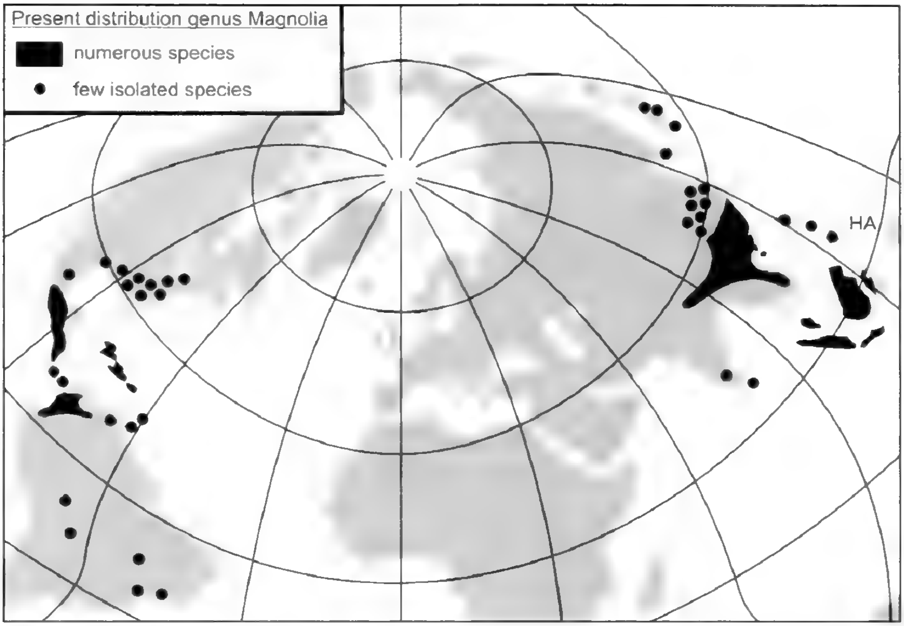


Fig. 1. Extant magnolias have a classic disjunct distribution in Southeast Asia and in the Americas between Canada and Brazil, and nowhere in between. (Source: Hebda & Irving 2004)

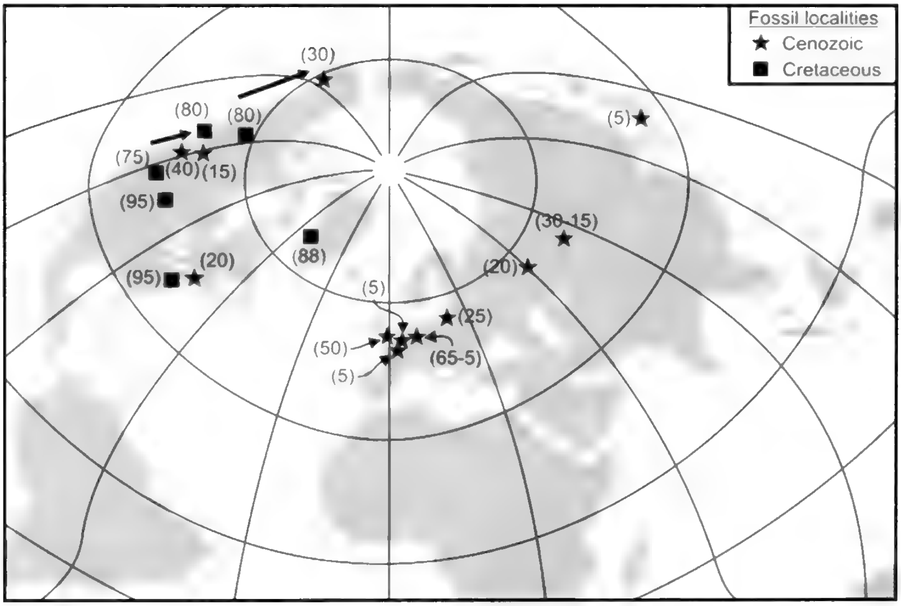


Fig. 2. Well established fossil occurrences of Cenozoic magnolias and Cretaceous ancestral taxa. Numbers in parentheses are approximate ages in millions of years. (Source: Hebda & Irving 2004)

virginiana L., the Laurel magnolia or Sweet bay. Magnolias are members of the Paleogene "boreotropical" flora. Magnolias flourished throughout the Cenozoic, and there are ancestral forms in the Late Cretaceous Epoch connecting them to one of the oldest lineages of flowering plants.

Taxonomy of modern Magnolias

Until recently, magnolias in the broad sense were divided among about half a dozen genera based on morphology and geographic isolation (Nooteboom 1993). There was much discussion concerning whether all these should be recognised as separate genera, the relationships among them, and the assignment of species to different genera (Nooteboom 1996, 2000). Recent studies of the position of flowers, the presence and absence of floral stipes (Figlar 2000), and especially of chloroplast DNA (cpDNA), have clarified relationships within the genus. Specifically, Figlar's study showed that morphological differences, once thought to separate *Magnolia* and *Michelia* L. are not valid, and cpDNA studies demonstrated that the variation within the genus *Magnolia*, as it was originally narrowly accepted, is greater than the variation among other closely related "genera" (Azuma et al. 2001, Kim et al. 2001).

This was later confirmed by study of nuclear DNA (Nie et al. 2008). For example, species in the old genus *Michelia* cluster closely with *Magnolia* species (Azuma et al. 2001, Kim et al. 2001). On the other hand, several species in the old section *Rhytidospermum* Spach, long considered to be indisputably magnolias, are, in fact, not closely related. Also, from the perspective of cpDNA as well as of nuclear DNA, western hemisphere (especially North American) species in the section *Rhytidospermum* appear to be the most diverse and basal in the cpDNA and in the nuclear DNA trees, suggesting that they could be relicts of the ancestral stock. Because there is evidence of ancient hybridisation, for instance several *Magnolia* species are polyploid, deep phylogeny cannot be deduced from chloroplast DNA, only from nuclear DNA.

Recent and historical geographical distribution of Magnolias

Molecular analyses reveal that several North American species are basal forms, suggesting that magnolias originated in North America, as indicated by their fossil record. We recognise four elements in their evolution.

(1) Ancestral magnolias originated in the Late Cretaceous of North America (Fig. 2) in the high mid-latitudes (45°–60°N), at low altitudes in a greenhouse climate.

Continental drift cannot be the sole factor in determining the distribution of extant magnolias, because reconstructing continents for Late Cretaceous and Paleogene epochs does not bring together the group's two principal zones of modern occurrence. Thus, Hebda & Irving (2004) made use of previous ideas concerning large changes

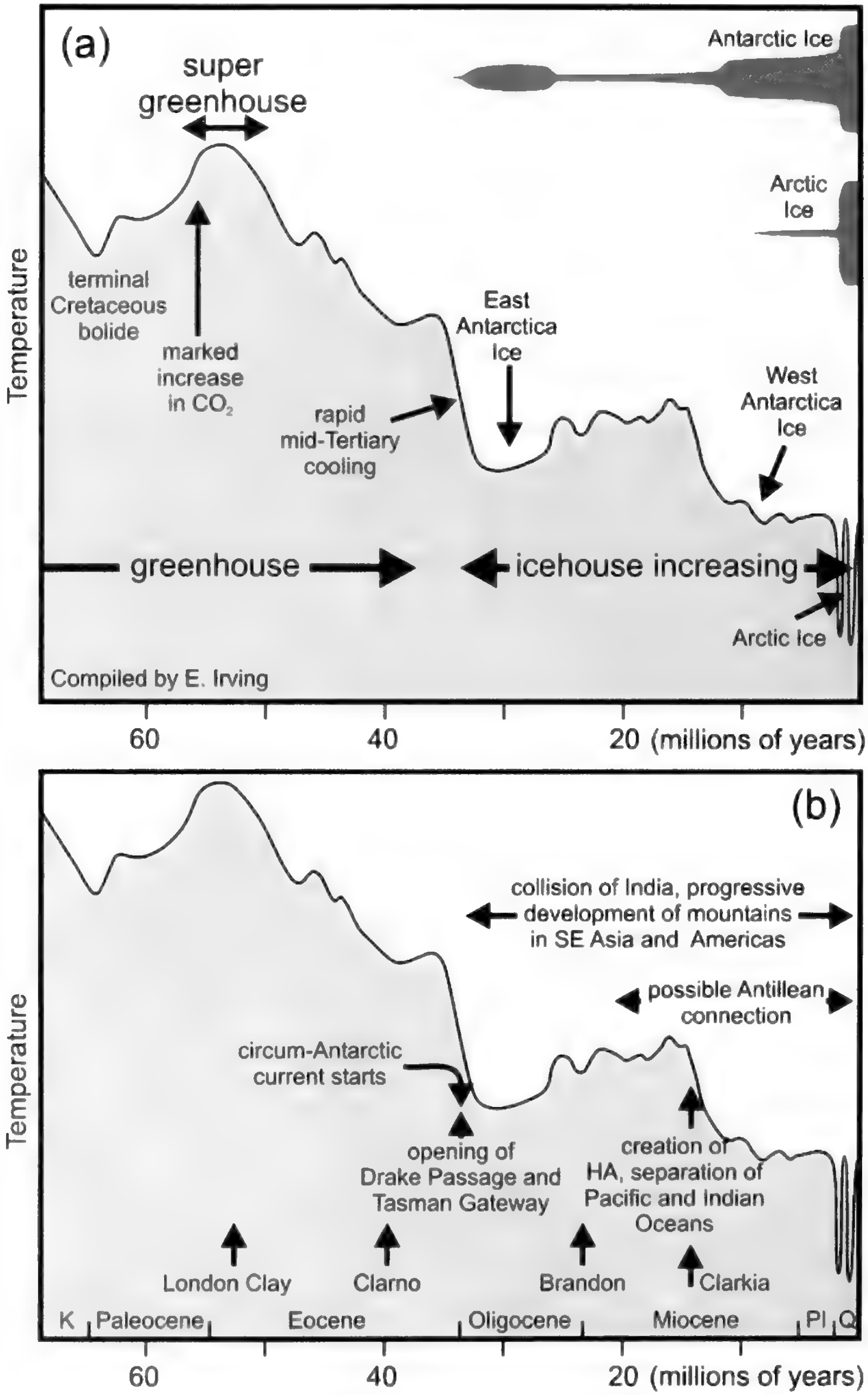


Fig. 3. Climatic (a) and paleogeographical (b) events during the past 70 Ma. HA = High Archipelago on the Sunda platform, Pl = Pliocene, Q = Quaternary. (London Clay, Clarno, Brandon and Clarkia are notable fossil magnolia localities). Compiled by E.I. Irving from various sources.

in the past distribution of moist warm temperate climate, and in the development of upland habitat.

These changes are linked to the Mid- and Late Cenozoic evolution of global climate from a non-glacial (greenhouse) to a glacial (ice-house) regime and to the contemporaneous creation of regions of moist, warm temperate climate in the newly uplifted mountains of the Americas, southeast Asia, and the High Archipelago on the Sunda Platform (Fig. 3).

The history of land masses is shown in Fig. 4, based on plate tectonics (for positions of continental lithosphere), paleomagnetic evidence (for geographical grid), and the distribution of terrestrial and marine sediments.

(2) During the exceptionally warm climate of the Eocene (Fig. 4b), magnolias spread eastwards, via the Disko Island and Thulean isthmuses, first to Europe, and then across Asia, still at low altitudes and high mid-latitudes.

The Thulean land-bridge remained almost continuous until the Miocene, and the remnant Disko Island volcanoes may have reduced the obstacle of the Labrador Sea. Cross-Atlantic migration routes may, therefore, have been open but were less hospitable than earlier.

(3) With mid-Cenozoic global cooling, they shifted to lower mid-latitudes (30°–45°N), eventually becoming extinct in Europe and southern Siberia, dividing a once continuous distribution into two, and becoming centred in eastern Asia and in North America.

(4) In the late Cenozoic, as ice-house conditions developed, magnolias migrated southward from both centres into moist warm temperate upland sites in the newly uplifted mountain ranges of South and Central America, southeast Asia, and the High Archipelago (Fig. 4e).

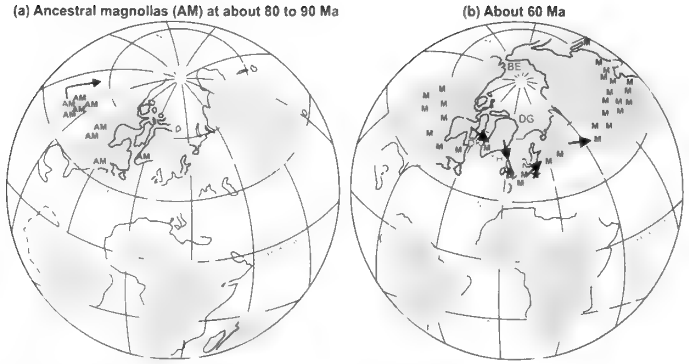
Thus the late Cenozoic evolution of magnolias is characterised by impoverishment of northern, and diversification of southern, species, the latter being driven by a combination of high relief and climate oscillations, and neither of the present centres of diversity is the centre of origin.

The evidence from DNA

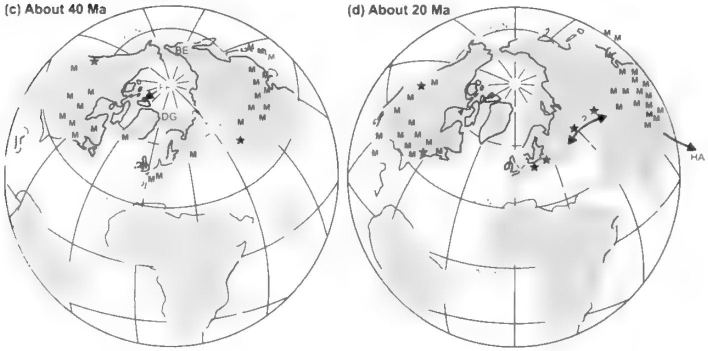
The divergence times for various major clades derived from a molecular (nuclear DNA) phylogenetic analysis of magnolias have been estimated by Nie et al. (2008). The relationship among the different groups is shown in Fig. 5. The major divergences include:

— *Liriodendron* L. and the rest of Magnoliaceae diverging c. 93 mya (*Liriodendron* then divided into two species c. 14 mya).

— The American section *Talauma* Baill., which is the base of all other magnolias, began diverging c. 54 mya. (The American species *Magnolia tripetala* L. is ancestral


(a) Ancestral magnolias (AM) at about 80 to 90 Ma

(b) About 60 Ma


(c) About 40 Ma

(d) About 20 Ma

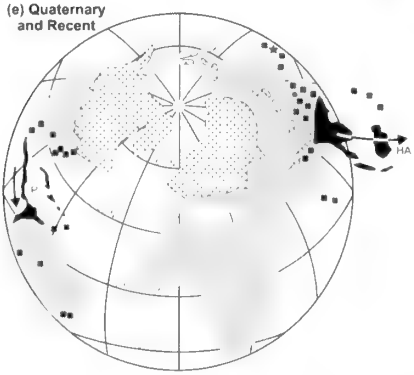

(e) Quaternary and Recent

Fig. 4. a. Possible latest Cretaceous northward migration of Vancouver Island shown. **b.** Distribution of possible magnolia sites with respect to land bridges. **c.** Slight cooling about 40 million years ago and a beginning of magnolia migration southwards. **d.** About 20 million years ago, magnolias have become nearly extinct in Europe, but *Yulania* Spach. seeds are found until c. 2 mya (Hebda & Irving 2004, v.d. Hammen et al. 1971). **e.** The deciduous, temperate species are derived from evergreen warm-temperate species as an adaptation to the climate. (Source: Hebda & Irving 2004). BE = Bering land bridge; DG = De Geer Landbridge; FF = Fossil Forest, Axel Heiberg Island; HA = High Archipelago on the Sunda platform; IP = Isthmus of Panama; M – possible *Magnolia* site; TH = Thulean landbridge; TS = Turgai Street; * = fossil *Magnolia*; crosses indicate fewer (often more isolated) species; black areas indicate numerous species present; stippled areas are maximum glaciated cover.

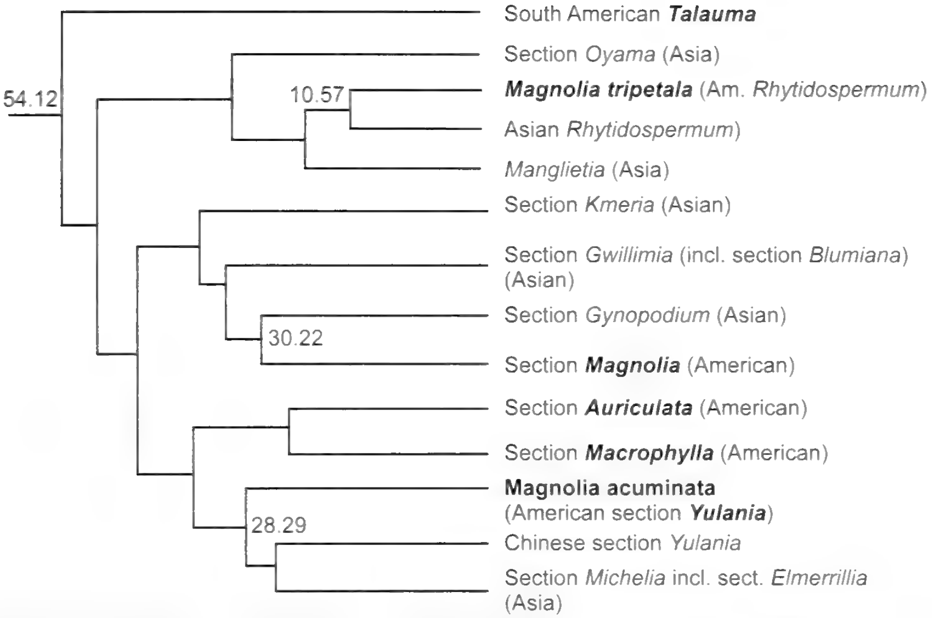


Fig. 5. A cladogram of the sections of which the nuclear DNA is known. Adapted from Fig. 6 of Nie et al. (2008).

to the other (Chinese) species of section *Rhytidospermum*, which began to diverge around 10 mya.)

— The Chinese *Magnolia sinica* (Y.W. Law) Noteboom and *Magnolia nitida* W.W. Sm. (section *Gynopodium*) are basal to section *Magnolia*, which diverged c. 30 mya. (This split happened probably in America. The American *M. virginiana* L. is basal to the rest of section *Magnolia*, which diverged as two groups c. 18 mya.)

— The American *Magnolia fraseri* Walter and *M. macrophylla* Michx., basal to both *Yulania* and *Michelia*, are clearly ancestral. *Magnolia acuminata* (L.) L., the only American *Yulania* species, is basal to both the rest of *Yulania* and *Michelia*, and diverged about 28 mya.

From such analyses, the resulting cladograms lead to the conclusion that Magnolioideae consists of only one genus, *Magnolia*. Even the subdivision into three subgenera is now obsolete. Apart from subg. *Magnolia*, only one other subgenus may be arguably recognised, *Yulania* Spach, consisting of five sections: the basal (American) sections *Auriculata* Figlar & Noot. and *Macrophylla* Figlar & Noot.; *Tulipastrum* (Spach) Figlar & Noot. with only the American *M. acuminata*; section *Yulania*; and section *Michelia*. Here the problem is that sections *Auriculata* and *Macrophylla* do not group morphologically with *Michelia* and *Yulania*.

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Spatial and temporal diversification of *Tetrastigma* (Vitaceae)

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ABSTRACT. The spatial and temporal diversification of *Tetrastigma* Planch., a genus of the grape family Vitaceae with a wide distribution throughout subtropical and tropical Asia to Australia, was examined through phylogenetic and biogeographic analyses. The times of divergence within *Tetrastigma* were estimated with the Bayesian approach based on sequence data from four plastid (*atpB-rbcL*, *rps16*, *trnL-F*, and *psbA-trnH*) markers using the computer program BEAST. The divergence time between *Tetrastigma* and its closely relative *Cayratia* was estimated as the early Eocene around 50.6 million years ago (mya), with 95% HPD: 36.3–65.3 mya. The age of the crown group of *Tetrastigma* was dated to be late Eocene (36.9 mya, with 95% HPD: 25.7–49.3 mya). Biogeographic analyses using LAGRANGE suggested that the Sino–Himalayan region (and the adjacent Indochina) was the most likely ancestral area for *Tetrastigma*. Most *Tetrastigma* species sampled from the Malesian region were nested within clades of the Sino–Himalayan and Indochina region. A few Malesian species primarily from SE Sulawesi, the Philippines and New Guinea are not associated with the Sino–Himalayan and Indochina species and formed separated clades. The results suggest that *Tetrastigma* species in the Malesian region have complex biogeographic origins and continental Asia served as an important source area for the Malesian members of the genus.

Keywords. BEAST, biogeography, dating, LAGRANGE, *Tetrastigma*, Vitaceae

Introduction

Tetrastigma Planch. is one of the 14 currently recognised genera of the grape family Vitaceae (Wen 2007). The genus contains approximately 95 species and has a wide distribution in tropical and subtropical Asia, extending to Australia, ranging from India to China, across SE Asia eastward to Fiji (Fig. 1; Chen et al. 2011). *Tetrastigma* is characterised by unbranched to digitately branched tendrils, a dioecious sexual system, and 4-lobed stigmas in female flowers (Wen 2007). *Tetrastigma* is well-known in Southeast (SE) Asia for being the host plants for all three genera of Rafflesiaceae, which contains the largest flower of the world (Meijer 1997, Barkman et al. 2004).

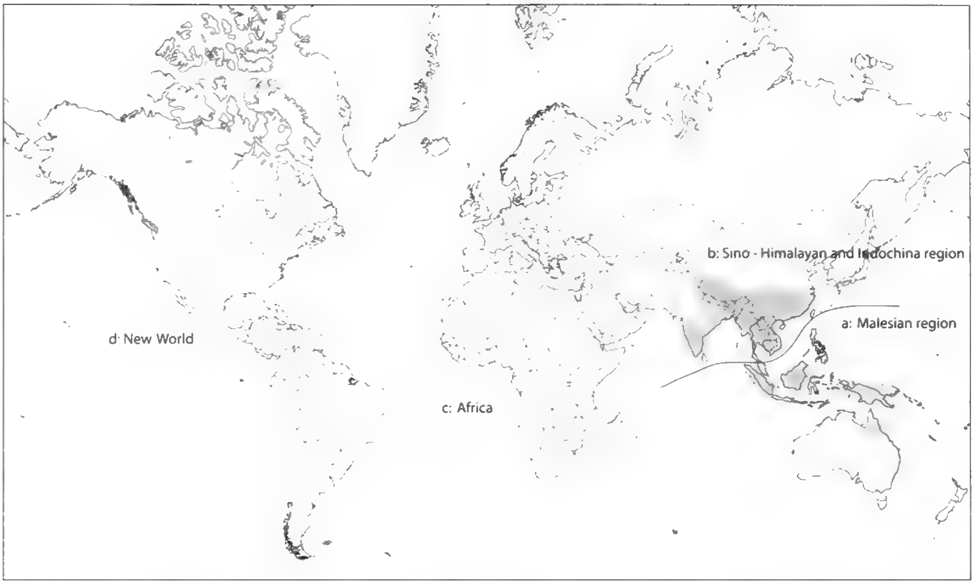

Fig. 1. The geographic distribution of *Tetrastigma* in Asia and Australia (gray area). "a–d" indicates four areas of endemism used in the LAGRANGE analysis: a, the Malesian region; b, Sino–Himalayan and Indochina region; c, Africa; and d, New World.

Recently the genus attracted more scientific attention with the reported horizontal gene transfer of mitochondrial genes (e.g., *nad1B-C* and *apt1*) from the *Tetrastigma* host to the parasite of *Rafflesia* R.Br. (Davis & Wurdack 2004, Barkman et al. 2007). Several species of the genus are widely cultivated as climbing ornamentals (Wen 2007). *Tetrastigma hemsleyanum* Diels & Gilg is an important Chinese folk medicine for treating hepatitis, fever, pneumonia, rheumatism, and sore throat (Liu et al. 2002).

Southeast Asia and the West Pacific have long attracted the attention of biogeographers. The waters of SE Asia contain the highest marine faunal diversity in the world (Briggs 1974; Paulay 1997). Biodiversity in this region shows several patterns of origin between two complicated palaeocontinents separated for a considerable period of time. Two main patterns have often been recognised: (1) a pattern of Southeast Asian elements (perhaps of Laurasian origin) and (2) a pattern of Australian elements (perhaps of Gondwanan origin). Some recent phylogenetic and biogeographic studies have shed important insights into the evolution of plant, insect, fish, and animal distribution patterns in this region (see Butlin et al. 1998; Marwick 2009; Clouse & Girbet 2010; Esselstyn & Oliveros 2010; Renner et al. 2010). Yet the Malesian flora comprises an estimated 42,000 plant species (Roos 1993), with only about 15% being revised during the last 50 years. Thus biogeographic analyses of more plant genera or lineages in this region are very much needed.

Several lines of evidence have shown that good dispersers such as some plants and insects from Eurasia can dominate the entire SE Asia and extend to the Pacific islands (Gressitt 1982, Baker et al. 1998). *Tetrastigma* is a good disperser, bearing berries and often dispersed by fruit-eating birds, bats and mammals (Tiffney &

Barghoorn 1976, Moran et al. 2009). The genus thus provides another opportunity to reconstruct the biogeographic diversification of plants in SE Asia and the West Pacific.

Tetrastigma is widely distributed in the Sino–Himalayan Indochina region and the Malesian region. The Malesian region comprises west Malesia (the Sunda shelf: Malay Peninsula, Sumatra, Borneo, and West Java), central Malesia (Wallacea: part of Java, the Philippines, Sulawesi, the Lesser Sunda Islands, and the Moluccas), and east Malesia (the Sahul Shelf: New Guinea) as subunits (van Welzen et al. 2005). The Wallace's line separates the west and the east Malesian flora, the transition area between west and east Malesia is known as Wallacea, i.e., central Malesia. The tectonic history of the Malesian region is complicated because of the two waves of Australian slivers moving towards the Eurasian plate. The first wave formed SE Asia and the west part of the Malay Archipelago to the Wallace's or the Weber's line around 90 million years ago (mya). The second wave made SE Asia collide with the West Pacific in the middle Miocene (van Welzen et al. 2003). Besides this complicated tectonic history and cycles of glacials, the origins of plant taxa may also be complex. It is still poorly known which taxa in this region dispersed from the Sino-Himalayan region or from the West Pacific region. Because species of *Tetrastigma* occupy the entire Malesian region, it seems a good model to test the dispersal pathways in the Malesian region.

The fossil records of the Vitaceae in the Northern Hemisphere during the Tertiary are well documented. Pollen, fruit, seed and leaf fossils have been recorded from the late Paleocene to the Pleistocene (Collinson 1983, Cervallos-Ferriz & Stockey 1990, Taylor 1990, Wheeler & Lapasha 1994). Fossil seeds of Vitaceae are commonly found in many Tertiary beds in the Northern Hemisphere (Reid & Chandler 1933; Kirchheimer 1939; Miki 1956; Dorofeev 1957, 1963; Chandler 1925, 1957, 1961a, 1961b, 1962, 1963, 1964, 1978; Tiffney & Barghoorn 1976; Chen & Manchester 2007). Because the fossils resemble extant seeds, these fossil seeds have usually been identified to extant genera (Chen & Manchester 2007). Many of those fossils were designated to the genus *Vitis* and others were included in *Ampelopsis*, *Ampelocissus*, *Parthenocissus*; yet only a few fossils were reported to be *Tetrastigma* and *Cayratia* (Tiffney & Barghoorn 1976, Chen & Manchester 2007, Chen 2009). In general, fossil seeds of Vitaceae were relatively diverse in Europe (Chen 2009). About 13 fossil species of *Tetrastigma* have been reported from the early Eocene to Pliocene (Kirchheimer 1938; Miki 1956; Chandler 1925, 1961ab, 1962; Reid & Chandler 1933; Teodoridis 2003). Most of them varied morphologically and were from Europe in the early Tertiary and only two species (*T. japonica* Miki and *T. tazimiensis* Miki) were from Asia (Japan) from the Pliocene. Chen & Manchester (2007) carefully examined the fossils of *Ampelocissus* concerning seed morphological characters. They questioned the generic assignment of most *Tetrastigma* fossil seeds, which resemble those of *Ampelocissus* and *Ampelopsis*. They transferred two *Tetrastigma* fossils to *Ampelocissus*: with *T. lobatum* Chandler now being *Ampelocissus lobatum* (Chandler) Chen & Manchester, and *Tetrastigma chandleri* now as *Ampelocissus chandleri* (Kirchheimer) Chen & Manchester (Chen & Manchester 2007). There may be no reliable *Tetrastigma* fossil seeds so far (S. Manchester, pers. comm.). Moreover, the oldest fossil in Vitaceae was *Ampelocissus parvisemina* Chen & Manchester from the late Paleocene of North Dakota and the early-middle Eocene of Oregon (Chen & Manchester 2007).

Chen et al. (2011) conducted a phylogenetic analysis of *Tetrastigma* using four plastid markers. Yet the biogeography of the genus has never been explored. The objectives of this study are to (1) estimate the divergence times of *Tetrastigma* clades, and (2) infer the biogeographic diversification history of the genus.

Materials and methods

Estimation of divergence times

Representatives from the entire grape family plus *Leea* were sampled to help date the ages of *Tetrastigma* and its relatives with both direct fossil and secondary calibrations in Vitales. Sequences used in the dating analysis are shown in Appendix A and were derived from a phylogenetic analysis of the genus by Chen et al. (2011). We used the Bayesian dating method based on a relaxed-clock model to estimate divergence times (Thorne et al. 1998; Thorne & Kishino 2002; Drummond et al. 2006). The Bayesian coalescent approach to estimate the times of each clade in *Tetrastigma* and their credibility intervals was implemented in the computer program BEAST version 1.4.7 (Drummond & Rambaut 2007), which employs a Bayesian Markov chain Monte Carlo (MCMC) to co-estimate topology, substitution rates and node ages. All analyses were performed using the GTR model of nucleotide substitution with a gamma and invariant sites distribution with four rate categories. The tree prior model (constant size) was implemented in the analysis, with rate variation across branches assumed to be uncorrelated and lognormally distributed (Drummond et al. 2006). The final estimates were obtained using the model that yielded the highest posterior probability. Posterior distributions of parameters were approximated using two independent MCMC analyses of 20,000,000 generations with 10% burn-in. Samples from the two chains which yielded similar results were combined and convergence of the chains was checked using the program Tracer 1.3 (Rambaut & Drummond 2004).

Ancestral area analyses

Reconstruction of ancestral areas on a phylogeny is important to understand the biogeographic diversification history of a lineage, as it permits the inference of the place of origin and dispersal routes of organisms. Dispersal-vicariance (DIVA; Ronquist 1996, 1997) analysis is often used to construct the biogeographic history. But for DIVA analyses the phylogeny of a group needs to be well resolved. The procedure used in the computer program LARANGE differs from the DIVA methods in that it allows a broader range of speciation models and also incorporates any available temporal information such as divergence times and dispersal opportunities. We thus employed the maximum likelihood-based method LAGRANGE (Ree et al. 2005, Ree & Smith 2008) to reconstruct the diversification of *Tetrastigma* and its close relatives. Four areas of endemism were defined according to their distribution: (a) the Malesian region, (b) the Sino–Himalayan and Indochina region, (c) Africa, and

(d) the New World. The maximum number of areas in ancestral ranges was set as two in LAGRANGE, as no species of Vitaceae is distributed in more than two areas of endemism.

Vitaceae fossil constraints

We constrained the ages of two nodes in the phylogeny of *Tetrastigma* and its close relatives in Vitaceae (Fig. 2). The stem lineage of *Ampelocissus* and *Vitis* was constrained to be 60 ± 5.0 mya old (node) in Fig. 2 based on fossil seeds of *Ampelocissus parvisemina* from the late Paleocene of North Dakota and the early to middle Eocene of Oregon (Chen & Manchester 2007). Wikström et al. (2001) reported the estimated divergence time between *Leea* and *Vitis* as 80–92 mya. Recently Magallón & Castillo (2009) suggested an older age from 90.65 (90.47–90.84) to 90.82 (90.64–91) mya for the origin of Vitaceae using different relaxed or constraint schemes, although there is no direct credible fossil evidence for Vitaceae or Leeaceae in the Cretaceous. It is curious that the distinctive seed morphology of this clade, readily observable in many Paleogene localities, is missing from well studied Cretaceous deposits. The inferences from Magallón & Castillo (2009) and Wikström et al. (2001) are close, although the latter were criticised for the nonparametric rate smoothing method and for calibrating their tree using only a single calibration point. Bell et al. (2010), however, suggested a time ranging from 65 (45–81) to 48 (21–79) Ma for the stem age of Vitaceae. Although their estimates were based on 36 fossil calibrations and a relaxed approach in dating the whole angiosperm groups, they seem to have underestimated the age for Vitaceae because the estimates were younger than the age suggested by fossil evidence (e.g., in Chen & Manchester 2007). We thus constrained the stem of Vitaceae to be 85 ± 5.0 mya (Fig. 2), a strategy similar to that of Nie et al. (2010). We did not use any *Tetrastigma* fossils from the Tertiary (Kirchheimer 1938; Miki 1956, Chandler 1925, 1961ab, 1962; Reid & Chandler, 1933; Teodoridis 2003), as Chen & Manchester (2007) questioned the placement of all these fossils in the genus.

Results

The chronogram of *Tetrastigma* and its relatives from Vitaceae based on combined plastid *atpB-rbcL*, *rps16*, *trnL-F*, and *psbA-trnH* data is shown in Fig. 2. The age of the *Tetrastigma* stem was estimated to be 50.6 mya (with a 95% highest posterior density [HPD] interval of 36.4–65.3 mya) in the early Tertiary. The crown age of *Tetrastigma* was estimated to be 36.94 mya (with a 95% HPD: 25.7–49.3 mya) approximately in the late Eocene. Node ages of eight major clades (clades A–H) are shown in Table 1. Clade B formed a well-supported clade with the large Clade A based on Bayesian analysis (Fig. 2). Three species (*T. glabratum Wen10670*, *T. lawsoni Wen7505*, *T. tuberculatum Wen10280*) in Clade B were collected from Java, Singapore, and SE Sulawesi. The crown age of Clade D was estimated to be 7.8 mya (95% HPD: 2.2–14.5 mya, node D in Fig. 2) including two endemic species of the Philippines (*T. ellipticum*, and *T. laxum*) and a new undescribed species collected from SE Sulawesi. The small Clade

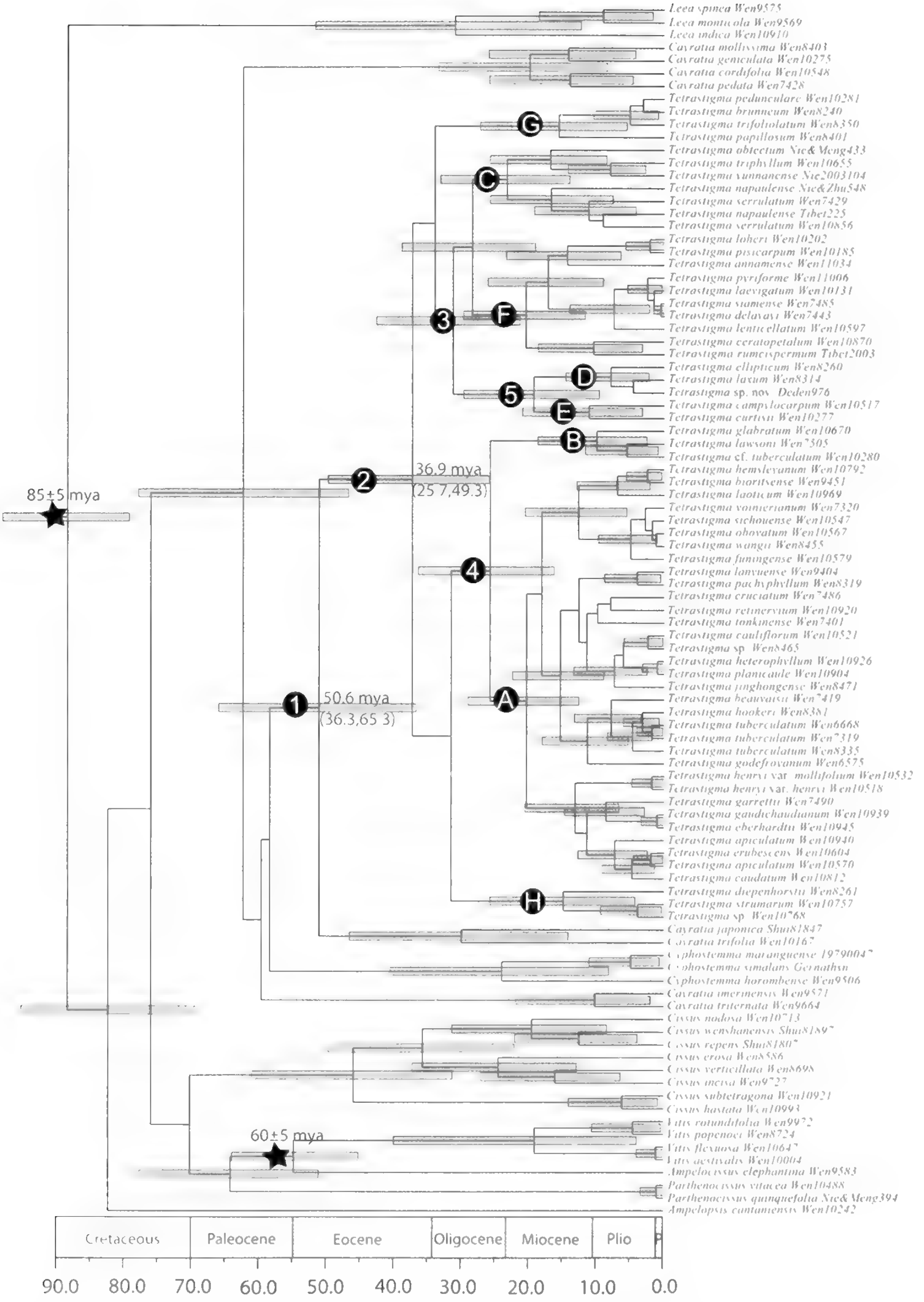

Fig. 2. Chronogram of *Tetastigma* and its relatives from Vitaceae based on combined plastid data (*atpB-rbcL*, *rps16*, *trnL-F*, and *psbA-trnH*) inferred from BEAST. Gray bars represent the 95% high posterior density credibility interval for node ages. Calibration points are indicated with black asterisks.

E was sister to Clade D with good Bayesian posterior probability support (node 5 in Fig. 2). Clade D only contained central Malesian species of *Tetrastigma*. However, the sister Clade E contained two biogeographically disjunct species, *T. campylocarpum* Planch. distributed from India to the Sino–Himalayan and Indochina region and *T. curtisii* (Ridl.) Suess. & Suess. of the Malesian region. The crown age of Clade E was estimated to be 11.0 mya (95% HPD: 3.1–20.8 mya, node E in Fig. 2). The ancestral area of Clade E was inferred to be widespread in the Sino–Himalayan and Indochina region and the Malesian region (node E in Fig. 3). Clade F included seven species from the Sino–Himalayan and Indochina region and three species from the Malesian region (*T. loheri Wen 10202* and *T. pisicarpum Wen 10185* from SE Sulawesi and *T. laevigatum Wen 10131* from West Java). The east and central Malesian *T. diepenhorstii Wen 10812* and west Malesian endemic *T. strumarum Wen 10757* and *T.* sp. *Wen10768* constituted Clade H (Fig. 3). The crown age of Clade H was estimated to be 14.8 mya (95% HPD: 4.2–25.6 mya, node H in Fig. 2) in the middle Miocene.

Reconstruction of ancestral areas with LAGRANGE suggested an ancestral distribution and early diversification of *Tetrastigma* in the Sino–Himalayan and Indochina region in Fig. 3. Subsequently, *Tetrastigma* species were dispersed from continental Asia to the Malesian region. The colonisation of the Sino–Himalayan and Indochina region occurred at nodes A and C and the colonisations of the Malesian region were supported by several nodes: B, D, G, and H (Fig. 3). The most widespread ancestral range appeared at nodes E and F (Fig. 3).

Table 1. Prior probability and posterior distribution estimates for *Tetrastigma* within the phylogenetic framework of Vitaceae. Mean dates were used as the divergence time of the nodes.

Node constrained and estimated	Posterior distribution Mean (mya)	95%HPD (mya)
Node 1	50.6	36.3–65.3
Node 2	36.9	25.7–49.3
Node 3	31.0	21.1–42.2
Node 4	25.5	16.1–36.1
Node 5	19.1	9.5–29.5
Node A	20.2	12.5–28.8
Node B	9.9	2.5–18.5
Node C	23.0	13.8–32.8
Node D	7.8	2.2–14.5
Node E	11.0	9.4–29.5
Node F	20.3	11.6–29.5
Node G	15.4	5.4–27.0
Node H	14.8	4.2–25.6

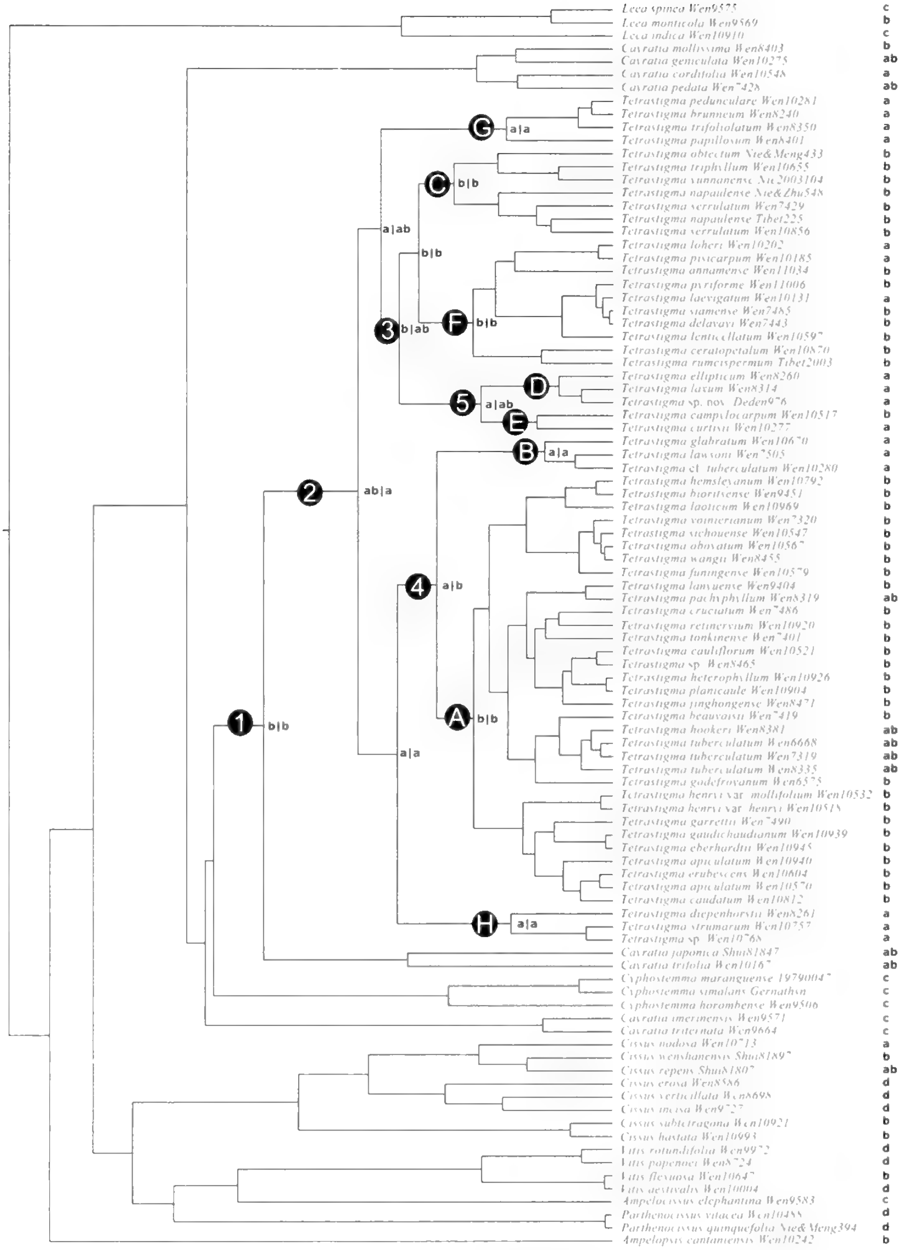

Fig. 3. Results of the LAGRANGE analysis of *Tetrastigma* and its close relatives. The tree was based on a 50% majority-rule consensus tree of a Bayesian Markov chain Monte Carlo (MCMC) analysis of the combined plastid data set. Estimated ancestral areas of the clades (Clades A–H) within *Tetrastigma* are shown on the nodes using circles (see details in the Discussion). The four areas of endemism are: a, the Malesian region; b, Sino–Himalayan and Indochina region; c, Africa; and d, New World. A slash in the result of LAGRANGE indicates the split of areas into two daughter lineages, i.e., left/right, where "up" and "down" are the ranges inherited by each descendant branch.

Discussion

Ancestral area and divergence times of Tetrastigma

Tetrastigma is distinctive in comparison with other genera of Vitaceae in its four-lobed stigma in female flowers and dioecious sexual system. Our phylogenetic analyses have suggested that *Tetrastigma* is nested within the genus *Cayratia* Juss. (also see Chen et al. 2011). *Tetrastigma* was estimated to have diverged from its closest relative in the early Eocene (50.6 mya, 95% HPD: 36.3–65.3 mya, node 1 in Fig. 2). The genus *Cayratia* is widely distributed in the Old World from Africa throughout Asia to Oceania. *Cayratia* has been shown to be paraphyletic (Rossetto et al. 2001, 2002, 2007; Ingrouille et al. 2002; Soejima & Wen 2006; Wen et al. 2007; Ren et al. 2011). Our analyses has divided the genus into three geographic clades: the African clade, and two clades in temperate to tropical Asia extending to Australia. *Tetrastigma* is sister to the clade including *Cayratia japonica* (Thunb.) Gagnep. and *C. trifolia* (L.) Domin, largely from temperate to tropical Asia. Thus, *Tetrastigma* may have originated in the Sino–Himalayan and Indochina region in the early Eocene.

The stem group of *Tetrastigma* is estimated to be 50.6 mya (95% HPD: 36.3–65.3 mya, node 1 in Fig. 2) approximately in the early Eocene. The crown of extant *Tetrastigma* is estimated to be 36.9 mya (95% HPD: 25.7–49.3 mya, node 2 in Fig. 2). The divergence of *Tetrastigma* species between the Sino–Himalayan and Indochina region and the Malesian region may have begun in the late Eocene. In our Bayesian analyses, at the beginning of *Tetrastigma* diversity, there are two Malesian clades (clades G and H in Fig. 2), and the Sino–Himalayan and Indochina and Malesian clades (clades A–F in Fig. 2). Improved understanding of SE Asia's physical history (Hall 2001, 2002; Metcalfe 2001; van Welzen 2005) suggests that only west Malesia (Malaysia, Sumatra, Borneo, Java, part of Sulawesi) was above water before the early Eocene. By the Miocene, the other islands (such as part of Sulawesi, Moluccas, part of the Lesser Sunda islands, and New Guinea) in the Malesian region got into their approximate present-day positions. With *Tetrastigma* fruits being dispersable berries, the migrations of *Tetrastigma* between the Sino–Himalayan and Indochina region and the Malesian region could have occurred at least three times, according to our results.

Biogeographic evolution of Tetrastigma in the Malesian region

Tetrastigma species from the Malesian region are scattered in six major clades (clades B, D, E, F, G, and H in Fig. 2). Some of the west and central Malesian *Tetrastigma* samples are nested within the clades of Sino–Himalayan and Indochina region (clades B, E, and F in Fig. 3). Thus, migrations of *Tetrastigma* species between the Sino–Himalayan and Indochina region and west Malesia may have occurred at least three times from the late Oligocene to the middle Miocene (Fig. 2). During these periods with climatic and sea level changes, species of *Tetrastigma* seem to have dispersed from the Sino–Himalayan / Indochina region to the Malesian region and also from the Malesian region back to the Sino–Himalayan / Indochina region.

Three species (*T. glabratum Wen 10670*, *T. lawsoni Wen 7505*, *T. tuberculatum Wen 10280*) in Clade B are widespread in Indochina and both west and central

Malesia. The divergence time between these two disjunctive clades is estimated to be 25.5 mya (95% HPD: 16.1–36.1 mya, node 4 in Fig. 2) in the late Oligocene and early Miocene. Throughout the Oligocene, a land connection between Borneo and Indochina was hypothesised to have existed (Pupilli 1973, Lloyd 1978). *Tetrastigma* species of the Sino-Himalayan and Indochina region may have dispersed into west and central Malesia through the land bridge or via direct long-distance dispersal. Furthermore, Clade F included seven species from the Sino–Himalayan and Indochina region as well as species from west and central Malesia (*T. loheri Wen 10202* and *T. pisicarpum Wen 10185* from SE Sulawesi and *T. laevigatum Wen10131* from West Java). Although the phylogeny did not well resolve the relationships within Clade F, the clade apparently represents another biogeographc connection between continental Asia and the Malesian region. The Oligocene and earliest Miocene were periods with much drier and cooler climates; a major climatic change occurred in the early Miocene (Morley & Flenley 1987), a period with markedly warm and moist climatic conditions through a large part of SE Asia and East Asia (also see Morley 1998). During this period, the ancestor of Clade A may have diversified rapidly in the Sino–Himalayan / Indochina region, with 50% of *Tetrastigma* species now endemic to this region (see Li 1998; Chen et al. 2011).

Dispersal of *Tetrastigma* ancestors between west and central Malesian region and the Sino–Himalayan / Indochina region may also be shown in Clade G and node 3 (Fig. 3). In Clade G, the basally branched taxon *T. papillosum* (Bl.) Planch. is widely distributed from southwestern China, Thailand, Southeast Asia to New Guinea. The other three species in this clade are distributed in three areas of Malesia. Species in Clade D included two endemic species of the Philippines (*T. ellipticum* and *T. laxum*) and a new species collected from SE Sulawesi. The clade thus showed a close biogeographic connection between the Philippines and Sulawesi. During the Neogene, a volcanic arc existed along the north arm of Sulawesi and possible island chain connections may have existed to the Philippines (Moss & Wilson 1998). Moreover, many authors (Duffels 1990, Musser 1987, Balgooy 1987) have noted that the flora and fauna of the south arm of Sulawesi are different from the rest of Sulawesi, which may be explained by the geologic evidence that during much of the Tertiary, South Sulawesi was below sea level. But the rifting and rotating of South Sulawesi (including SE Sulawesi at present) and its accretion to North Sulawesi just occurred 10 mya ago (Hall 1998). With a global warm phase during the middle Miocene (Fulthorpe & Schlanger 1989), it is possible for migration through those island chains and connection lands between the Philippines and Sulawesi, i.e., west Malesia and central Maleisa. Species endemic to central Malesia formed Clade D, sister to Clade E (Fig. 3) and nested with the Sino–Himalayan and Indochina region species. The ancestral area of Clade E is inferred to be the Sino–Himalayan and Indochina region and Malesian region (node E in Fig. 3). The crown age of Clade E is estimated to be 11.0 mya (95% HPD: 3.1–20.8 mya, node E in Fig. 2) in the middle Miocene. Two species are included in Clade E (Fig. 3), *T. campylocarpum* Planch. widely distributed from India to the Sino–Himalayan / Indochina region and *T. curtisii* (Ridl.) Suess. & Suess. occurring in west and central Malesia. Thus, the possible dispersal route of *Tetrastigma* species is most likely from the Sino–Himalayan/Indochina region to west Malesia in the early Oligocene (node 3 in Fig. 2) and then to central Malesia after the middle Miocene (node 5 in Fig. 2).

Clade H contains the east Malesian and Papuan species of *Tetrastigma* (Fig. 3). The basally branching species of Clade H is *T. deipenhorstii* (Miq.) Latiff, a widespread species in west Malesia. It is probable that the east Malesian species dispersed from west Malesia. Our results are consistent with routes from the Sino–Himalayan / Indochina region to west Malesia and from west to central Malesia.

We need to test our hypotheses of *Tetrastigma* biogeography with additional sampling in both the Sino-Himalayan Indochina region and the Malesian region and with improved resolution of the phylogeny and finer division of the areas of endemism. Nevertheless, our initial results add another case study on the complex biogeographic origins of Malesian plant taxa, and support the idea that continental Asia served as an important source area for the Malesian members of the genus.

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Appendix A. Taxa and accessions used for dating and biogeographic analysis of *Tetrastigma* and the outgroup taxa of Vitaceae and Leeaceae with their GenBank numbers. "–" indicates missing data. All voucher specimens are deposited at the US National Herbarium (US).

Species	Collection localities (and vouchers)	GenBank accessions *atpB-rbcL, rps16, trnL-F, psbA-trnH*
Ampelocissus elephantina Planch.	Madagascar, Antsiranana (*J. Wen 9583*)	HM585516, HM585792, HM585932, HM585659
Ampelopsis cantoniensis Planch.	Indonesia, SE Sulawesi (*J. Wen 10242*)	HM585517, HM585793, HM585933, HM585660
Cayratia cordifolia C.Y. Wu ex C.L. Li	China, Yunnan (*J. Wen 10548*)	HM585518, HM585794, HM585934, HM585661
Cayratia geniculata Gagnep.	Indonesia, SE Sulawesi (*J. Wen 10275*)	HM585519, HM585795, HM585935, HM585662
Cayratia imerinensis (Baker) Desc.	Madagascar, Antsiranana (*J. Wen 9571*)	HM585520, HM585796, HM585936, HM585663
Cayratia japonica (Thunb.) Gagnep.	China, Yunnan (*Y.-M. Shui 81836*)	HM585521, HM585797, HM585937, HM585664
Cayratia mollissima Gagnep.	Malaysia, Pahang (*J. Wen 8403*)	HM585522, HM585798, HM585938, HM585665
Cayratia pedata Gagnep.	Thailand, Chiang Mai (*J. Wen 7428*)	HM585523, HM585799, HM585939, –
Cayratia trifolia (L.) Domin	Indonesia, SE Sulawesi (*J. Wen 10167*)	HM585524, HM585800, HM585940, HM585666
Cayratia triternata (Baker) Desc.	Madagascar, Antsiranana (*J. Wen 9664*)	HM585525, HM585801, HM585941, HM585667
Cissus erosa Rich.	Peru, Arequipa (*J. Wen 8586*)	HM585526, HM585802, HM585942, HM585668
Cissus hastata Planch.	Vietnam, Danang (*J. Wen 10993*)	HM585527, HM585803, HM585943, HM585669
Cissus incisa Des Moul.	USA, Texas (*J. Wen 9727*)	HM585528, HM585804, HM585944, HM585670
Cissus nodosa Blume	Indonesia, Papua (*J. Wen 10713*)	HM585529, HM585805, HM585945, HM585671
Cissus repens Lam.	China, Yunnan (*Y.-M. Shui 81807*)	HM585530, HM585806, HM585946, HM585672
Cissus subtetragona Planch.	Vietnam, Ninh Binh (*J. Wen 10921*)	HM585531, HM585807, HM585947, HM585673
Cissus verticillata (L.) Nicolson & C.E. Jarvis	Mexico, Chiapas (*J. Wen 8698*)	HM585532, HM585808, HM585948, HM585674

Cissus wenshanensis C.L. Li	China, Yunnan (*Y.-M. Shui 81897*)	HM585533, HM585809, HM585949, HM585675
Cyphostemma horombense Desc.	Madagascar, Fianarantsoa (*J. Wen 9506*)	HM585534, HM585810, HM585950, HM585676
Cyphostemma maranguense (Gilg) Desc.	National Botanic Garden of Belgium (cult.) (*19790047*)	HM585535, HM585811, HM585951, HM585677
Cyphostemma simulans (C.A.Sm.) Wild & R.B. Drumm.	USA, Iowa (cult.) (*J. Gerrath s.n.*)	HM585536, HM585812, HM585952, HM585678
Leea indica (Burm.f.) Merr.	Vietnam, Ninh Binh (*J. Wen 10910*)	HM585537, HM585813, HM585953, HM585679
Leea monticola J. Wen	Madagascar, Antsiranana (*J. Wen 9569*)	HM585538, HM585814, HM585954, –
Leea spinea Desc.	Madagascar, Antsiranana (*J. Wen 9575*)	HM585539, HM585815, HM585955, –
Parthenocissus vitacea (Knerr) Hitchc.	China, Yunnan (cult.) (*Z.-L. Nie & Y. Meng 394*)	HM585540, HM585816, HM585956, HM585680
Parthenocissus vitacea (Knerr) Hitchc.	Canada, Quebec (*J. Wen 10488*)	HM585541, HM585817, HM585957, HM585681
Tetrastigma annamense Gagnep.	Vietnam, Lam Dong (*J. Wen 11034*)	HM585543, HM585819, HM585959, HM585683
Tetrastigma apiculatum Gagnep.	Vietnam, Hoa Binh (*J. Wen 10940*)	HM585546, HM585822, HM585962, HM585686
Tetrastigma apiculatum Gagnep.	China, Yunnan (*J. Wen 10570*)	HM585544, HM585820, HM585960, HM585684
Tetrastigma beauvaisii Gagnep.	Thailand, Mae Hong Son (*J. Wen 7419*)	HM585547, HM585823, HM585963, HM585687
Tetrastigma bioritsense (Hayata) Hsu & Kuoh	China, Taiwan (*J. Wen 9451*)	HM585548, HM585824, HM585964, HM585688
Tetrastigma brunneum Merr.	Philippines, Luzon (*J. Wen 8240*)	HM585549, HM585825, HM585965, HM585689
Tetrastigma campylocarpum Planch.	China, Yunnan (*J. Wen 10521*)	HM585552, HM585828, HM585968, HM585692
Tetrastigma caudatum Merr. & Chun	Vietnam, Vinh Phuc (*J. Wen 10812*)	HM585551, HM585827, HM585967, HM585691
Tetrastigma cauliflorum Merr.	China, Yunnan (*J. Wen 10521*)	HM585552, HM585828, HM585968, HM585692

Tetrastigma ceratopelatum C.Y. Wu	Vietnam, Lao Cai (*J. Wen 10870*)	HM585558, HM585834, HM585974, HM585698
T. cf. *tuberculatum*	Indonesia, SE Sulawesi (*J. Wen 10280*)	HM585559, HM585835, HM585975, HM585699
Tetrastigma cruciatum Craib & Gagnep.	Thailand, Chiang Mai (*J. Wen 7486*)	HM585562, HM585838, HM585978, HM585702
Tetrastigma curtisii (Ridl.) Suesseng.	Indonesia, SE Sulawesi (*J. Wen 10277*)	HM585563, HM585839, HM585979, HM585703
Tetrastigma delavayi Gagnep.	Thailand, Chiang Mai (*J. Wen 7443*)	HM585565, HM585841, HM585981, HM585705
Tetrastigma diepenhorstii (Miq.) Latiff	Philippines, Luzon (*J. Wen 8261*)	HM585567, HM585843, HM585983, HM585707
Tetrastigma eberhardtii Gagnep.	Vietnam, Ninh Binh (*J. Wen 10945*)	HM585568, HM585844, HM585984, HM585708
Tetrastigma ellipticum Merr.	the Philippines, Luzon (*J. Wen 8260*)	HM585569, HM585845, HM585985, HM585709
Tetrastigma erubescens Planch.	China, Yunnan (*J. Wen 10604*)	HM585570, HM585846, HM585986, HM585710
Tetrastigma funingense C.L. Li	China, Yunnan (*J. Wen 10579*)	HM585574, HM585850, HM585990, HM585714
Tetrastigma garrettii Gagnep.	Thailand, Chiang Mai (*J. Wen 7490*)	HM585578, HM585854, HM585994, HM585718
Tetrastigma glabratum Planch.	Indonesia, West Java (*J. Wen 10670*)	HM585580, HM585856, HM585996, –
Tetrastigma godefroyanum Planch.	China, Hainan (*J. Wen 6575*)	HM585581, HM585857, HM585997, HM585719
Tetrastigma gaudichaudianum Planch.	Vietnam, Hoa Binh (*J. Wen 10939*)	HM585583, HM585859, HM585999, HM585721
Tetrastigma hemsleyanum Diels & Gilg	Vietnam, Ninh Binh (*J. Wen 10792*)	HM585585, HM585861, HM586001, HM585723
Tetrastigma henryi (Gagnep.) var. *henryi* Gagnep.	China, Yunnan (*J. Wen 10518*)	HM585586, HM585862, HM586002, HM585724
Tetrastigma henryi (Gagnep.) var. *mollifolium* W.T. Wang	China, Yunnan (*J. Wen 10532*)	HM585587, HM585863, HM586003, HM585725
Tetrastigma heterophyllum Gagnep.	Vietnam, Ninh Binh (*J. Wen 10926*)	HM585588, HM585864, HM586004, HM585726

Tetrastigma hookeri Planch.	Malaysia, Pahang (*J. Wen 8381*)	HM585589, HM585865, HM586005, HM585727
Tetrastigma jinghongense C.L. Li	China, Yunnan (*J. Wen 8471*)	HM585590, HM585866, HM586006, HM585728
Tetrastigma laevigatum Gagnep.	Indonesia, West Java (*J. Wen 10131*)	HM585591, HM585867, HM586007, HM585729
Tetrastigma lanyuense C.E. Chang	China, Taiwan (*J. Wen 9404*)	HM585593, HM585869, HM586009, HM585731
Tetrastigma laoticum Gagnep.	Vietnam, Guangnam (*J. Wen 10969*)	HM585595, HM585871, HM586011, HM585733
Tetrastigma lawsoni (King) Burkill	Singapore (*J. Wen 7505*)	HM585599, HM585874, HM586015, HM585737
Tetrastigma laxum Merr.	Philippines, Luzon (*J. Wen 8314*)	HM585602, HM585877, HM586018, HM585740
Tetrastigma lenticellatum C.Y. Wu ex W.T. Wang	China, Yunnan (*J. Wen 10597*)	HM585604, HM585879, HM586020, HM585742
Tetrastigma loheri Gagnep.	Indonesia, SE Sulawesi (*J. Wen 10202*)	HM585605, HM585880, HM586021, HM585743
Tetrastigma napaulense (DC.) C.L. Li	China, Xizang (*Tibet 225*)	HM585607, HM585882, HM586023, HM585745
Tetrastigma napaulense (DC.) C.L. Li	Nepal, Kathmandu (Z.-L. *Nie & W.-D. Zhu 548*)	HM585606, HM585881, HM586022, HM585744
Tetrastigma obovatum Gagnep.	China, Yunnan (*J. Wen 10567*)	HM585608, HM585883, HM586024, HM585746
Tetrastigma obtectum (Wall.) Planch.	China, Guizhou (*Z.-L. Nie & Y. Meng 433*)	HM585612, HM585886, HM586027, HM585750
Tetrastigma pachyphyllum (Hemsl.) Chun	Philippines, Luzon (*J. Wen 8319*)	HM585616, HM585891, HM586032, HM585753
Tetrastigma papillosum Planch.	Malaysia, Pahang (*J. Wen 8401*)	HM585617, HM585892, HM586033, HM585754
Tetrastigma pedunculare Planch.	Indonesia, SE Sulawesi (*J. Wen 10281*)	HM585620, HM585895, HM586036, HM585757
Tetrastigma pisicarpum (Miq.) Planch.	Indonesia, SE Sulawesi (*J. Wen 10185*)	HM585621, HM585896, , HM585758
Tetrastigma planicaule Gagnep.	Vietnam, Ninh Binh (*J. Wen 10904*)	HM585622, HM585897, HM586037, HM585759
Tetrastigma pyriforme Gagnep.	Vietnam, Lam Dong (*J. Wen 11006*)	HM585623, –, HM586038, HM585760
Tetrastigma retinervium Planch.	Vietnam. Vinh Phuc (*J. Wen 10920*)	HM585625, HM585899, HM586040, HM585762

Tetrastigma rumicispermum Planch.	China, Yunnan (*Tibet 2003*)	HM585626, HM585900, HM586041, HM585763
Tetrastigma serrulatum Planch.	Vietnam, Lao Cai (*J. Wen 10856*)	HM585628, HM585902, HM586043, HM585765
Tetrastigma serrulatum Planch.	Thailand, Chiang Mai (*J. Wen 7429*)	HM585629, HM585903, HM586044, HM585766
Tetrastigma siamense Gagnep. & Craib	Chiang Mai (*J. Wen 7485*)	HM585630, HM585904, HM586045, HM585767
Tetrastigma sichouense C.L. Li	China, Yunnan (*J. Wen 10547*)	HM585631, HM585905, HM586046, HM585768
Tetrastigma sp. nov.	Indonesia, SE Sulawesi (*G. Deden 976*)	HM585640, HM585913, HM586055, HM585777
Tetrastigma sp.	China, Yunnan (*J. Wen 8465*)	HM585639, HM585912, HM586054, HM585776
Tetrastigma sp.	Indonesia, West Papua (*J. Wen 10768*)	HM585637, HM585910, HM586052, HM585774
Tetrastigma strumarum Gagnep.	Indonesia, Papua (*J. Wen 10757*)	HM585641, HM585914, HM586056, HM585778
Tetrastigma tonkinense Gagnep.	Thailand, Chiang Mai (*J. Wen 7401*)	HM585642, HM585915, HM586057, HM585779
Tetrastigma trifoliolatum Merr.	Malaysia, Selangor (*J. Wen 8350*)	HM585644, HM585917, HM586059, HM585781
Tetrastigma triphyllum (Gagnep.) W.T. Wang	China, Yunnan (*J. Wen 10655*)	HM585648, HM585921, HM586063, HM585783
Tetrastigma tuberculatum (Blume) Latiff	USA, Missouri Bot. Gard. (cult.) (*J. Wen 6668*)	HM585649, HM585922, HM586064, HM585784
Tetrastigma tuberculatum (Blume) Latiff	USA, Illinois (cult.) (*J. Wen 7319*)	HM585650, HM585923, HM586065, –
Tetrastigma tuberculatum (Blume) Latiff	Malaysia, Selangor (*J. Wen 8335*)	HM585651, HM585924, HM586066, HM585785
Tetrastigma voinierianum Pierre ex Pit.	USA, Illinois (cult.) (*J. Wen 7320*)	HM585652, HM585925, HM586067, HM585786
Tetrastigma wangii J. Wen	China, Yunnan (*J. Wen 8455*)	HM585653, HM585926, HM586068, HM585787
Tetrastigma yunnanense Gagnep.	China, Yunnan (cult.) (*Z.-L. Nie 2003104*)	HM585654, HM585927, HM586069,
Vitis aestivalis Michx.	USA, South Carolina (*J. Wen 10004*)	HM585655, HM585928, HM586070, HM585788

Vitis flexuosa Thunb.	China, Yunnan (*J. Wen 10647*)	HM585656, HM585929, HM586071, HM585789
Vitis popenoei J.L. Fennell	Mexico, Chiapas (*J. Wen 8724*)	HM585657, HM585930, HM586072, HM585790
Vitis rotundifolia Michx.	USA, Virginia (*J. Wen 9972*)	HM585658, HM585931, HM586073, HM585791

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The floristic position of Java

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ABSTRACT. Floristically, Java was always considered to be west of Wallace's line together with the Malay Peninsula, Sumatra, Borneo, the Philippines and Sulawesi. Recently, statistical analyses of rough geographic data per species (presence or absence on islands or island groups) showed that Java is part of the central Wallacean area in Malesia (together with also the Philippines, Sulawesi, the Lesser Sunda Islands, and the Moluccas) rather than of Sundaland (restricted to the Malay Peninsula, Sumatra, and Borneo). More precise distribution maps for Java with collecting localities show that most species are widespread over Java or show a (more) western distribution; few species show an eastern distribution. The distributions show strong correlations with altitude (mountain species) and with precipitation (roughly wet in the west, dry in the east). The expectation was to find mainly species with a drought preference (Wallacean). However, most species show a preference for a wet distribution, which is related to a Sunda distribution. The fact that the statistical tests used for the first database show a Wallacean connection for Java probably is the result of the relative values these test use instead of absolute numbers, e.g., the resemblance between, especially, the flora of the Lesser Sunda Islands with Java is very high.

Keywords. Flora Malesiana, floristics, Java, Malesia

Introduction

In 1859 Wallacea introduced his famous zoological boundary, Wallace's line (Huxley 1868), that divided the Malay Archipelago (or Malesia: Steenis 1950; Raes & Welzen 2009) into an eastern and western part. Wallace's line runs east of the Philippines, then either west (Wallace 1859, 1863–1876) or east (Wallace 1860, 1910) of Sulawesi (also known as Celebes), and ends between Bali and Lombok in the Lesser Sunda Islands. Wallace discussed the position of Sulawesi in his book 'Island life' (Wallace 1880), in which he calls Sulawesi an 'anomalous island' with no continental connections as Sulawesi lacks Sundaic groups and contains (old) endemic and Australasian species. A more complete historical overview is presented in Simpson (1977) and George (1981), who both show that a number of variants of Wallace's line have been proposed based on the study of different groups of organisms (Fig. 1). The area encompassed by these lines is often called Wallacea, a term coined by Dickerson (1928), for an area already delimited by Wallace in 1863. The areas to the west (Malay Peninsula, Sumatra, Java, Borneo) and to the east (New Guinea) are referred to as the Sunda Shelf and the Sahul Shelf, respectively.

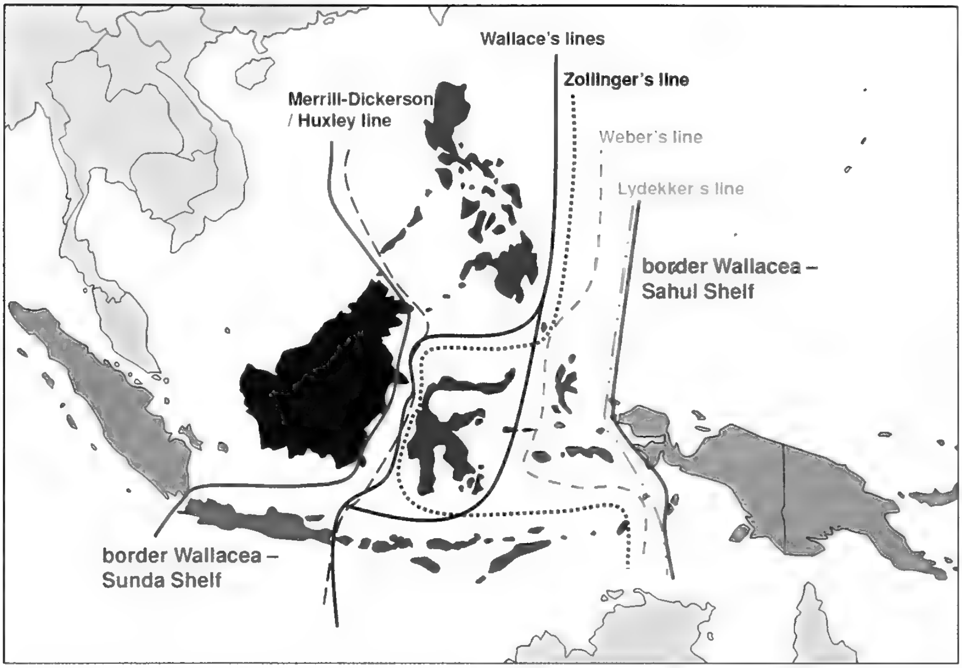

Fig. 1. Interpretations of Wallace's lines around Sulawesi and various alternatives are depicted in shades of blue. Red lines show the borders between the Sunda Shelf, Wallacea and the Sahul Shelf resulting from analyses discussed in the text.

Almost only zoological data were used to distinguish the lines (George 1981), and unsurprisingly, most botanist did not use the various boundaries. Steenis (1950) used distributions of plant genera when he contemplated the limits of the Malesian region, and based on the same data Wallace's line did not appear to be a distinct boundary in plant distributions. Welzen et al. (2005) used a limited floristic species database to show that all lines do form distinctive boundaries in plant distributions, each line stopping at least twice as many taxa as passing. Welzen & Slik (2009) even indicated which families are mainly responsible for the distribution patterns in Malesia. Only 20 families determine the patterns. Dipterocarpaceae, Fagaceae, and Nepenthaceae have their centre of diversity on the Sunda Shelf; Ericaceae, Monimiaceae, and Sapindaceae are typical for the Sahul Shelf; Araliaceae, Boraginaceae, Convolvulaceae, Cyperaceae, Dioscoreaceae, Lamiaceae, Loranthaceae, Mimosaceae, and Moraceae are predominantly Wallacean, and Burseraceae, Caesalpiniaceae, Flacourtiaceae, Meliaceae, and Myristicaceae show no distinct centre.

Recently, Welzen et al. (2011) analysed the distribution data per island group of all species published in Flora Malesiana series 1 (Angiosperms) and the Malesian orchids in Orchids Monograph (for island groups see Fig. 1). Various phenetic techniques were used: Principal Components Analysis, Fig. 2A; Non-metric Multidimensional Scaling analysis, Fig. 2B; a cluster analysis, Unweighted Pair Group Method with Arithmetic mean, Fig. 2C; and Kroeber's coefficient, the mean floral similarity between pairs of areas, Fig. 2D. All results show that Java is not west of Wallace's line, but east of it (Fig. 2). The tests were repeated for 100 randomly drawn matrices with equal contributions of all areas (500 species per area), which should nullify the effect of different island sizes (large islands like Borneo and New Guinea harbour far more (endemic) species than other areas and are then automatically separated from the rest in the analyses). Also, the analyses of the 100 matrices showed the same result for Java, not a part of the Sunda Shelf areas, but part of Wallacea. Thus, the borders between the three areas, Sunda Land/Shelf, Wallacea and Sahul Land/Shelf, have to be redrawn a bit (red lines in Fig. 1).

The Kroeber's Coefficient (Fig. 2D) nicely shows that in fact the botanical relationship between Java and Wallacea just wins in the other three analyses (PCA, NMS, UPGMA) from a Sunda relationship, because Java has a high floral mean resemblance (Fig. 3) with on the one hand Sumatra and the Malay Peninsula (Sunda Land) and on the other hand a slightly higher mean resemblance with the Lesser Sunda Islands and Sulawesi (Wallacea). The floral resemblance with Borneo (Sunda) and the Philippines and Moluccas (Wallacea) is somewhat less. Welzen et al. (2011)

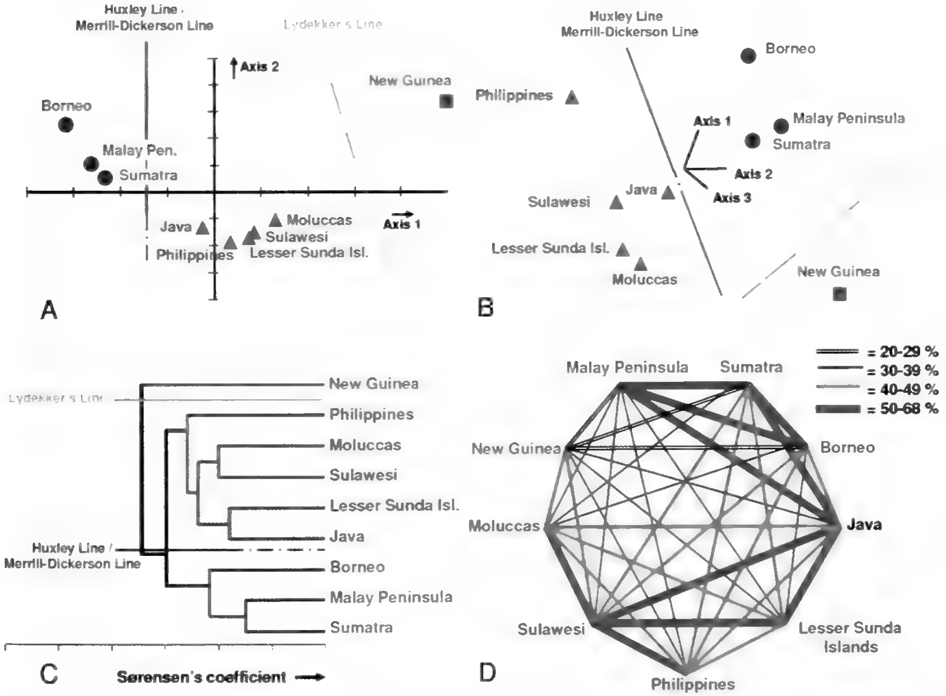

Fig. 2. The results of various phenetic tests on a database with presence absence data per island group for indigenous species revised in Flora Malesiana and Orchid Monographs. All tests place Java together with Wallacean areas. **A.** Principle Components Analysis (PCA). **B.** Non-metric Multidimensional Scaling analysis (NMS). **C.** Unweighted Pair Group Method with Arithmetic mean (UPGMA). **D.** Kroeber's coefficients with a mean floral similarity between pairs of areas indicated by various thicknesses of the lines connecting the pairs.

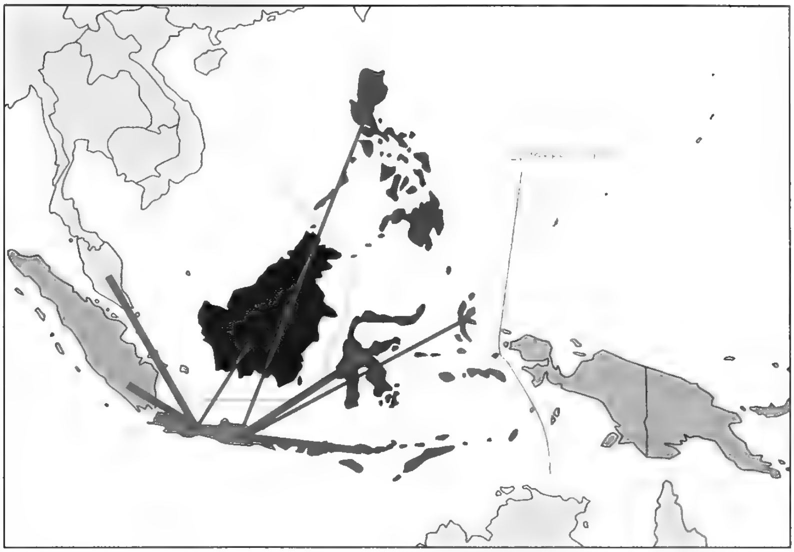

Fig. 3. Kroeber's coefficients between Java and the Sunda and Wallacean areas showing a high resemblance, on the one hand, with Sumatra and the Malay Peninsula on the Sunda Shelf; and, on the other hand, with the Lesser Sunda Islands and Sulawesi within Wallacea. Blue lines depict the borders of Wallacea.

discuss that the floral resemblances can largely be explained by the supposed savannah corridors running from the Malay Peninsula along and over Sumatra to Java during glacial periods. Via this corridor species that prefer a yearly dry period could disperse and are now still found in areas with a yearly dry monsoon.

The purpose of this paper is threefold: - establish why plant distributions more strongly point to a Wallacean relationship for Java; - check which kind of phenetic distribution patterns exist witin Java; and - explain these.

Materials and methods

In previous studies (Welzen et al. 2005, Welzen & Slik 2009, Welzen et al. 2011), a database was used whereby the presence and absence of indigenous species revised in Flora Malesiana series 1 and Orchid Monographs was noted for the Malay Peninsula, Sumatra, Java, Borneo, the Philippines, Sulawesi, Lesser Sunda Islands, Moluccas, and New Guinea. The areas used necessitated two alterations for two lines. The Merrill-Dickerson variant of the Huxley line runs officially between Palawan and the rest of the Philippines. This line is now considered to run between Palawan and Borneo (Fig. 1). Also, Wallace's line ends between Bali and Lombok in the Lesser Sunda Islands; this is redrawn between Java and Bali (Fig. 1). These redrawn lines are used in this study.

For this study, a database was created with collecting localities of species that are represented by digitised herbarium specimens from Java. Up to now, the database contains 97 families and 447 genera. The families starting with A or B are fully digitised, plus a part of C (26 families), some of the other families have also been digitised (e.g., Euphorbiaceae, Rhamnaceae, Sapindaceae, Vitaceae), but most other families are only partly digitised. The localities were georeferenced with the websites http://earth-info.nga.mil/gns/html/index.html and http://www.fallingrain.com/world/. Only the species with five or more different localities were included in the analysis, fewer localities were considered too incomplete to infer a distribution pattern. In total 808 species were sorted visually into different distribution patterns. This appeared to be rather straightforward. Four patterns were discriminated: 1) widespread over the island; 2) a western distribution (subdivided into 2a purely west, 2b west plus a few dots in central Java, and 2c west up to central Java; these three were not always distinctive); 3) a (central to) eastern distribution; and 4) a west-and-east-only distribution. All distributions were divided into low and high (above 1000 m) altitude.

The dot maps were produced with MapInfo Professional 7.0 (© MapInfo Corporation), the altitudinal and precipitation maps were made with Manifold GIS (Manifold.net), for which the datasets were obtained from the WorldClim 30 arc-second dataset (www.worldclim.org).

Results

Table 1 shows how many species were found per pattern. A large part, 49%, of the sampled plant species is widespread over Java (Fig. 4A). This group was not used in further analyses as they did not convey any information concerning a possible split of Java into the Sunda or Wallacean realms. It is possible to split off from this group plants typical for mangroves and beaches/dunes. A total of 273 species (Table 1) show a predominantly western distribution (Fig. 4B–D), some only in the extreme west (123 species, Fig. 4B), others with a few specimens in central Java (97 species, Fig. 4C)

Table 1. Numbers of species per pattern, divided for low, high or all altitudes. The western pattern is subdivided into three sub-patterns (shown in italics). The percentage is the percentage of 808 species.

Pattern	< 1000 m alt.	> 1000 m alt.	All altitudes	Total	%	Fig.
Widespread	288	36	72	396	49%	4a
West – Central	175	64	34	273	34%	
West	*76*	*37*	*10*	*123*	*15%*	4b
West (- Central)	*61*	*18*	*18*	*97*	*12%*	4c
West – Central	*38*	*9*	*6*	*53*	*7%*	4d
West and East	57	14	17	88	11%	4e
Central – East	36	10	5	51	6%	4f

or spread from west up to central Java (53 species, Fig. 4D). The opposite pattern, (central to) east Java also exists (51 species, Fig. 4F). The most curious distribution is perhaps the west and east distribution (88 species, Fig. 4E), whereby the species are absent in central Java.

Fig. 5A shows the mean amounts of yearly precipitation; western Java up to the central part, with the exception of the northern rim, plus the areas around the mountains in east Java are relatively wet, whereas the northern rim and the eastern

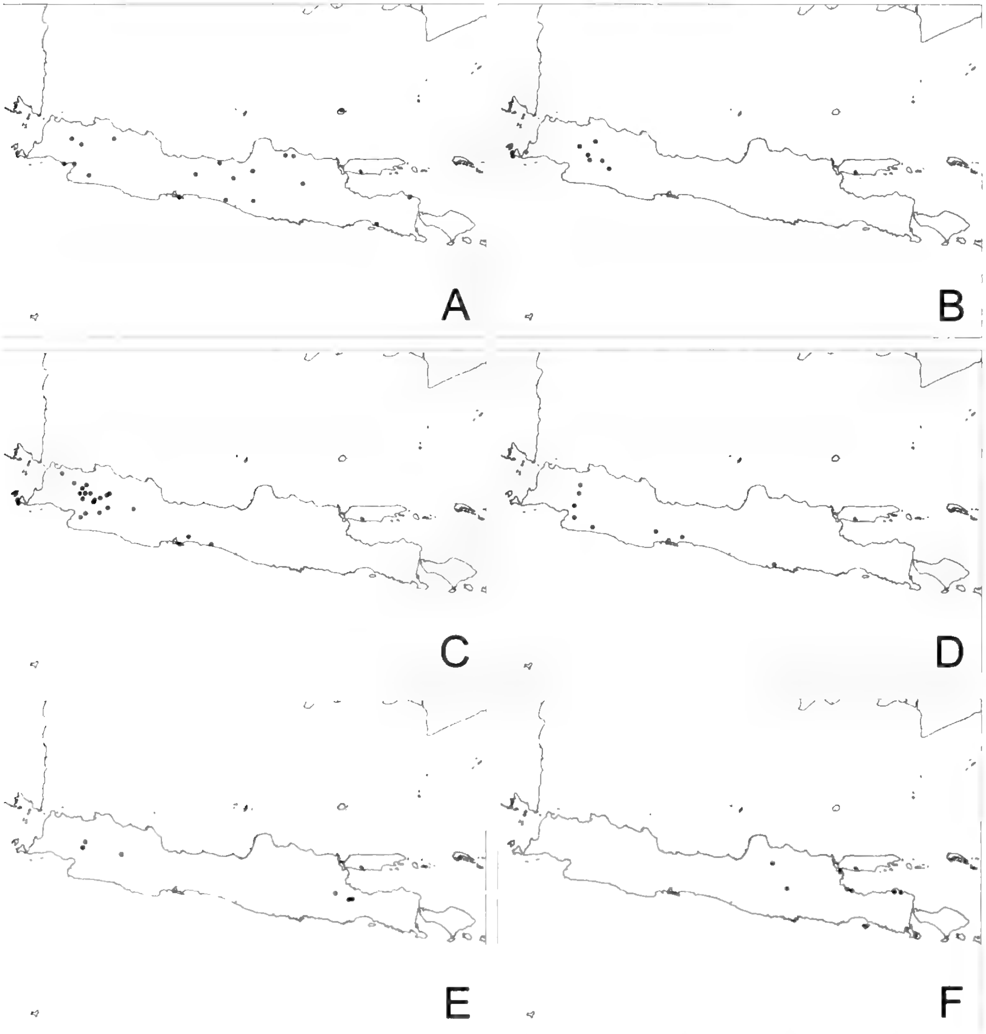

Fig. 4. Examples of the different distribution patterns, all low altitude. — **A.** *Maranthes corymbosa* Blume (Chrysobalanaceae/Rosaceae): widespread. **B.** *Pometia pinnata* J.R.Forst. & G.Forst. (Sapindaceae): west. **C.** *Kibara coriacea* (Blume) Tul. (Monimiaceae): West (– Central). **D.** *Cayratia japonica* (Thunb.) Gagnep. (Vitaceae): West – Central. **E.** *Epipogium roseum* (D.Don) Lindl. (Orchidaceae): West and East. **F.** *Capparis pubiflora* DC. (Capparaceae): Central – East.

half are much drier. Fig. 5B shows the mountains on Java. There is a row of volcanoes along the central axis of the island with a concentration of mountains in especially the western part. The low-altitude distributions correlate very well with the precipitation map (Fig. 5A). The western distributions are present in the wetter areas (demonstrated by the red dots of *Kibara coriacea*; Fig. 5A). The same correlation with wet areas is shown by the west and east distributions (grey dots of *Epipogium roseum*; Fig. 5A), in the west they are in the wet areas, in the east in the wet areas around the mountains. The eastern patterns show a correlation with low amounts of rain (blue dots of *Capparis pubiflora*; Fig. 5A).

The high-altitude distributions show a good correlation with the altitudinal map. Fig. 5B shows with red dots the distribution of the widespread *Sarcococca pruniformis* Lindl., and with blue dots the west and east distribution of *Dendrobium tetraedre* (Blume) Lindl. These species are present on the slopes of the mountains and thus also in areas with a higher precipitation.

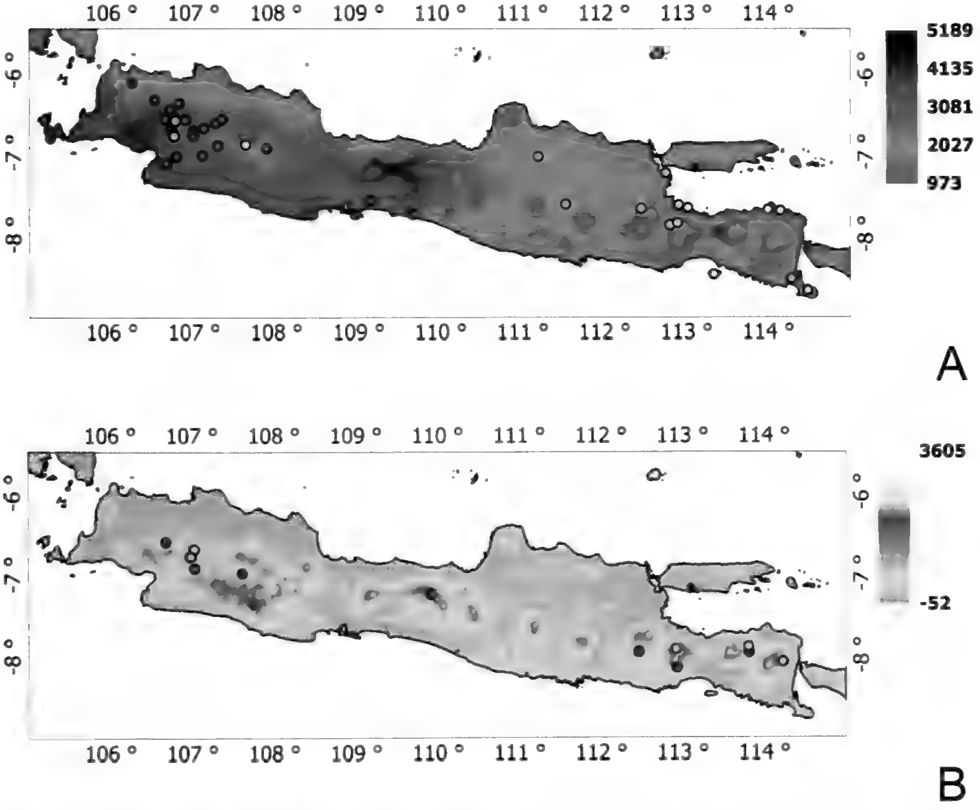

Fig. 5. A. Map of Java showing the mean annual precipitation in mm, ranging from 973 mm per year (brownish yellow) to 5189 mm (dark green). Red dots represent the distribution of *Kibara coriacea* (Blume) Tul. (Fig. 4C), green dots are *Capparis pubiflora* DC. (Fig. 4F); and grey dots are *Epipogium roseum* (D.Don) Lindl. (Fig. 4E). **B.** Map of Java showing altitude in m; red dots: *Sarcococca pruniformis* Lindl. (Buxaceae); blue dots: *Dendrobium tetraedre* (Blume) Lindl. (Orchidaceae); both are species of higher altitudes.

Discussion

The Sunda Shelf is characterised by an everwet climate, while most areas in Wallacea have a dry monsoon during part of the year (Steenis 1979). Thus, the distributions correlating with high(er) precipitation, the western (Fig. 4B–D; 5A: red dots), west and east (Fig. 4E, 5A: grey dots) and higher altitudinal distributions (Fig. 5B) point at a Sunda element in the flora of Java, while the distributions correlated with a dry monsoon, the eastern distributions (Fig. 4F, 5A: red dots), show the Wallacean influence. From Table 1 it follows that most species show a Sunda distribution pattern, while in the introduction it was explained that the highest floristic bonds are with the Wallacean areas (Fig. 2). How can we explain this apparent discrepancy?

The sample used might be too small. Up to now only the Javanese collections of the families starting with "A" or "B" have been fully digitised and georeferenced. These families might be biased towards a western distribution. The database will be extended in the future to cover all Javanese collections. The bias is probably absent, because Araliaceae and Boraginaceae, representing typical Wallacean elements (Welzen & Slik 2009; see introduction), are already included in the sample.

Dot maps only show places that were visited by collectors. All distributions are incomplete, because many places have never been visited or sampled. This problem can be overcome by applying species distribution or ecological niche modelling (e.g., Raes 2009), whereby environmental variables are correlated with the conditions present at the collecting localities and these are extrapolated to possibly suitable, non-sampled areas. These models may perhaps show a more Wallacean correlation. However, this is not expected as the dot maps already infer such a high correlation with precipitation and altitude.

One might argue that redrawing Wallace's line between Java and Bali, instead of between Bali and Lombok, caused the close floristic bonds between Java and the Lesser Sunda Islands. A possible high floral resemblance between Java and Bali may obscure the gap in floral elements between Bali and the rests of the Lesser Sunda Islands. However, this is not the case, because Bali is (as far as plants are concerned) much under-sampled in comparison to Java and the two other provinces in the Lesser Sunda Islands. The specimen database in the Leiden herbarium (L) shows 44,038 specimens for Java, only 728 for Bali, and 6,180 for the rest of the Lesser Sunda Islands.

Table 2 provides another explanation. Java shares a very high percentage of its flora with Sumatra and the Malay Peninsula (74% with each), but from the viewpoint of Sumatra and the Malay Peninsula this is far less (48% and 39%, respectively). For the Lesser Sunda Islands and Sulawesi this is different, they share 78% and 56% of their flora, respectively, with Java, while slightly more than 50% of the Javanese flora is present in the Lesser Sunda Islands and Sulawesi. Thus, based on percentages the shared flora between Java and the Wallacean areas is higher than with Sunda Land. However, when total numbers of species are compared (first column of Table 2), then Java shares more species with Sumatra and the Malay Peninsula than with Wallacea. The statistical tests discussed in the introduction (Welzen et al. 2011; Fig. 2) use

Table 2. Floristic overlap between Java and the various other islands: the first column shows the number of shared species between Java and one of the other regions; the second column the percentage overlap from the perspective of the other region; and the third column the percentage overlap from the perspective of Java. Thus Java and Sumatra share 999 species, which is 48% of Sumatra's flora and 74% of Java's flora. The numbers of species were obtained from a database with presence absence data per island group for all Malesian indigenous species published in Flora Malesiana ser. I and in Orchid Monographs.

Region	No. Spp.	% Region	% Java
Sumatra	999	48	$\boxed{74}$
Malay Peninsula	831	39	$\boxed{74}$
Borneo	773	28	57
Lesser Sunda Islands	702	$\boxed{78}$	52
Sulawesi	683	$\boxed{56}$	51
Philippines	762	41	57
Moluccas	490	52	36
New Guinea	581	20	43

relative numbers in their analyses. Therefore, it is not surprising that the tests placed Java in the Wallacean realm, while total numbers point at a Sunda connection.

The West and East disjunct distributions are not easily explained. They may be a result of glacial–interglacial cycles. During glacial periods the sea levels dropped and altitudinal floral zones on mountains became much lower, probably providing continuous ranges or stepping stones for dispersal and as a result, continuous, non-disjunct distributions. During interglacial periods, like present day, sea levels are much higher, just like the altitudinal floral zones on mountains. Seemingly, especially in central Java, species have disappeared, perhaps due to adverse conditions on the central mountains. This may also have happened to species now only restricted to higher altitudes in west Java: these may have been widespread during glacial periods, but disappeared in central and east Java during interglacial periods. An alternative explanation might be that the human influence in especially central Java was much higher than in east and west (probably not realistic as most people live in west Java) or that there has been less sampling in especially central Java.

Conclusions

Java shows a kind of floristic Janus head. On the one hand, based on total numbers of shared species, Java clearly has a Sunda Shelf relationship with especially Sumatra and the Malay Peninsula (Table 2, column 1). On the other hand, when relative numbers are used, then the higher resemblance with especially the flora of the Lesser Sunda

Islands and, to a lesser extent, that of Sulawesi, places Java in the Wallacean realm.

The distributions in Java mainly show a western or eastern component. The western distributions correlate with a high(er) amount of rainfall, the eastern distributions with a preference or tolerance for a drier climate. The higher altitudinal distributions correlate with the presence of volcanoes on Java.

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Colonisation and diversity of epiphytic orchids on trees in disturbed and undisturbed forests in the Asian tropics

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ABSTRACT. Orchids are the most diverse group of epiphytes with more than two thirds of all their species being epiphytic, yet they are comparatively little studied. Colonisation, diversity and distribution of epiphytic orchids and their phorophytes (supporting trees) at 72 sites in disturbed and undisturbed natural forests of south-eastern Bangladesh were studied within a 21,070 km^2 area. No evidence of phorophyte specificity was found, but some phorophyte species were preferred. Most phorophytes (76%) bore only a single species of orchid in one clump. Both orchid and phorophyte species were diverse but 30% of epiphytic orchid species were restricted to a single tree. Larger trees and trees in richer orchid areas accumulated more orchids. Colonisation by an epiphytic orchid is a rare and random event, the presence of one orchid neither attracting nor repelling others on the same phorophyte. The data suggest that the frequency of colonisation by epiphytic orchids is primarily a function of the age of the phorophyte (with greater age allowing both more time and more surfaces to accumulate seeds on them) and the existing orchid richness of an area (allowing for a higher colonisation rate from local seed input). Selective logging of the oldest trees in an area would therefore cause a decline in epiphytic orchid abundance and further loss in orchid richness of the area.

Keywords. Colonisation, diversity, epiphytes, orchids, tropical forests

Introduction

It has been estimated that 24,000 or more vascular plant species are epiphytes (Kress 1986). Epiphytes predominantly occur in tropical and subtropical regions (Benzing 1986). According to Huda et al. (1999), there are 106 epiphytic and 56 terrestrial orchids in Bangladesh and later on, it was estimated 116 epiphytic, 60 terrestrial, one saprophytic and one amphibious species of orchid were found (Huda 2007). Orchids are the most diverse group of epiphytes, about 70% of their species being epiphytic (Gentry & Dodson 1987, Gravendeel et al. 2004).

The availability of suitable phorophytes (supporting trees) is believed to have a strong influence on orchid distribution (Withner 1974). Orchid populations are generally small and composed of scattered or clustered individuals (Ackerman 1986). The numbers of orchids based on the number of different clumps on phorophytes have been studied by Johansson (1974) and Catling et al. (1986) but they did not consider the size of the clump or the height at which they grew. Phorophyte age and area available for colonisation may also affect epiphyte abundance and community composition (Catling et al. 1986). Moreover, phorophyte architecture such as canopy structure, branching pattern, leaf size, etc., may have strong influences on the germination and establishment of epiphytes (Benzing 1986). More recently, Werneck & Espirito-Santo (2002) and Garcia-Suarez et al. (2003) studied the structure, distribution and abundance of vascular epiphytes at different heights and in relation to the 'diameter at breast height' (dbh) of the phorophyte. However, the height of epiphytic orchids on phorophytes may be an important factor related to pollinator visitation. Some publications have specifically studied the richness and distribution of epiphytic species (Madison 1977, Cardelus et al. 2006) but while these studies include some orchids, to our knowledge, no recent detailed studies of epiphytic orchids have been reported. Several other researchers have included some orchids in general studies of epiphytes (Lebrun 1937, Johansson 1974, Catling et al. 1986, Michaloud & Michaloud-Pelletier 1987, Benzing 1990, Bogh 1992, Zimmerman & Olmsted 1992, Tremblay et al. 2006). Among the most detailed studies of epiphytic orchids are those of Went (1940), Hosokawa (1957) and Johansson (1974) in the forests of Indonesia, Micronesia and West Africa, respectively. The distribution, colonisation and association of epiphytic orchids in Belize were studied by Catling et al. (1986), and orchid-phorophyte relationships in a forest watershed in Puerto Rico were studied by Migenis & Ackerman (1993).

The aims of the present work were to detail the diversity and distribution of epiphytic orchids over a wider geographical area in both disturbed and undisturbed natural forests and to determine their colonisation pattern and the diversity of phorophytes.

Materials and methods

Study sites

The study area extends over 21,070 sq. km and a general field survey was conducted in 72 different sites of Chittagong, Cox's Bazar, Rangamati, Bandarban and Khagrachari districts of south-east Bangladesh. Occurrences on roadside trees were excluded in this study. Three different forest types were also specially studied. One of the forests (Sitapahar reserve forest in Rangamati district) was a natural mixed-species forest, while the others have been replanted after logging. Dariardighi in Cox's Bazar district was planted in the 1940s and Perachar in Khagrachari district was planted in the 1980s; both these sites also had some residual mature trees from before the last logging. In both forests, trees were being logged since the last replanting.

Methods

Epiphytic orchid diversity and frequency of occurrence were generally studied in 72 sites, as well as three different one-hectare quadrats in south-east Bangladesh. Epiphytic orchid species were recorded from orchid-bearing trees at all sites. The studied sites were selected on the basis of the number of reserved forests and relatively undisturbed vegetation units in the respective districts, which resulted in uneven sample sizes. Both big areas with less studied sites (e.g., Bandarban) and smaller areas with more studied sites (e.g., Cox's Bazar) were included.

Access to tree crowns was achieved with a ladder or by climbing the trees with help of local tree climbers. Inaccessible branches were also examined with the help of binoculars. Specimens of all orchid species were collected from the study areas during fieldwork. Collected specimens were identified by consulting the literature and known specimens available at K, E and ABD. Due to difficulties in determining sterile specimens, small samples were taken from each and grown in the Orchidarium of Chittagong University until flowering. Voucher specimens of all species were deposited in the Herbarium of Chittagong University (HCU). The epiphytic orchid-bearing phorophytes (supporting trees) were identified in the field and specimens of unidentified phorophyte trees were collected for later identification.
The epiphytic orchid diversity index for a particular area was calculated by using the following formula, following the IUCN SSC Orchid Specialist Group (1996):

$$\text{Orchid diversity index} = \frac{\text{Total number of orchid species}}{\text{Total area (sq. km)}} \times 1000$$

Numbers of clumps individual phorophyte and clump sizes of epiphytic orchids were recorded in the field. Due to the irregular structure and size of the different orchids, clumps were also divided into three groups, 1) small clumps of 1 5 pseudobulbs or stem shoots, 2) medium clumps of 6–20 pseudobulbs or stem shoots, and 3) large clumps of more than 20 pseudobulbs or stem shoots (Huda 2000). Even very large 1–2 m spreading clumps were considered as a single large clump when all parts remained connected.

The clump height on the phorophyte tree above the forest floor and diameter at breast height (dbh) were also recorded for each individual phorophyte. Clump height of orchids was measured by using a clinometer. The lower portion of the clump was considered in measuring the height. In hilly areas, metre-graduated bamboo sticks were used to measure height above the ground. The dbh was measured using diameter tape.

In the three one-hectare quadrats, all trees >5 m tall were sampled. Within each quadrat, all trees and orchid species were identified either in the field or in the laboratory. The number of clumps individual phorophyte, clump size, height of orchid clumps above the ground and dbh for trees within the quadrats were also recorded from all three forest areas.

Analyses

Statistical analyses including the χ^2 test, Yates correction, Poisson distribution, t-test, correlation and ANOVA by Post hoc test (LSD and Tukey test) were performed with Microsoft Excel and SPSS version 13.

Results

Distribution of epiphytic orchids

A total of 41 different epiphytic orchid species were recorded from the 72 sites. The scientific name authorities of orchids are given in Fig. 1, those of phorophyte tree species in Fig. 3. The distribution of the study sites, the total number of different epiphytic orchids encountered, and the orchid diversity index of each district are presented in Table 1. In spite of uneven sample sizes, Cox's Bazar was the richest area for epiphytic orchids with the highest diversity index and was much more diverse than the average for the whole region; whereas Khagrachari (a slightly bigger district with a similar number of sites studied) was the poorest area with the lowest diversity index. This may give some indication that the richness sampled has not been unduly influenced by area or number of study sites.

Orchid diversity and colonisation

The 41 orchid species were found on a total of 287 trees in the 72 studied sites. Most orchid species are infrequent in their occurrence on phorophytes. *Aerides odoratum, Cymbidium aloifolium* and *Bulbophyllum lilacinum* were the most frequently encountered on 66, 59 and 39 phorophytes, respectively, and 12 orchid species were found to be present on only one individual phorophyte (Fig. 1). Only 8% of the orchid species were found on less than 10 phorophyte trees. Among them, *Aerides odoratum* and *Cymbidium aloifolium,* are the commonly occurring species.

The distribution of number of epiphytic orchid clumps per tree among the phorophyte trees is illustrated in Fig. 2. Most phorophytes bore only a single orchid

Table 1. Total number of epiphytic orchid species found to occur in the 72 studied sites in 5 different districts of south east Bangladesh. The epiphytic orchid diversity index was calculated according to the IUCN/SSC Orchid Specialist Group (1996).

Parameters	District name					Total
	Chittagong	Cox's Bazar	Rangamati	Bandarban	Khagrachari	
Total no. of orchid species	22	26	17	16	07	41
Total area (sq. km)	5283	2492	6116	4479	2700	21070
No. of sites studied	14	13	22	11	12	72
Epiphytic orchid diversity index	4.16	10.43	2.78	3.57	2.59	3.42

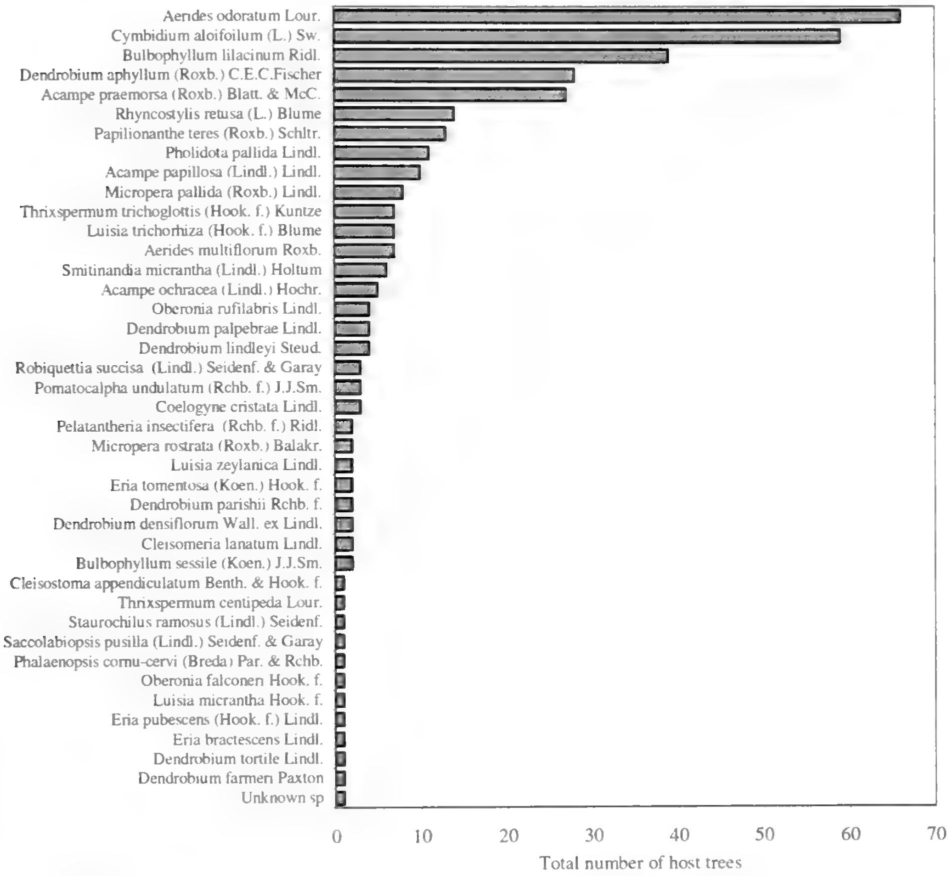

Fig. 1. Number of phorophyte trees associated with the different epiphytic orchid species.

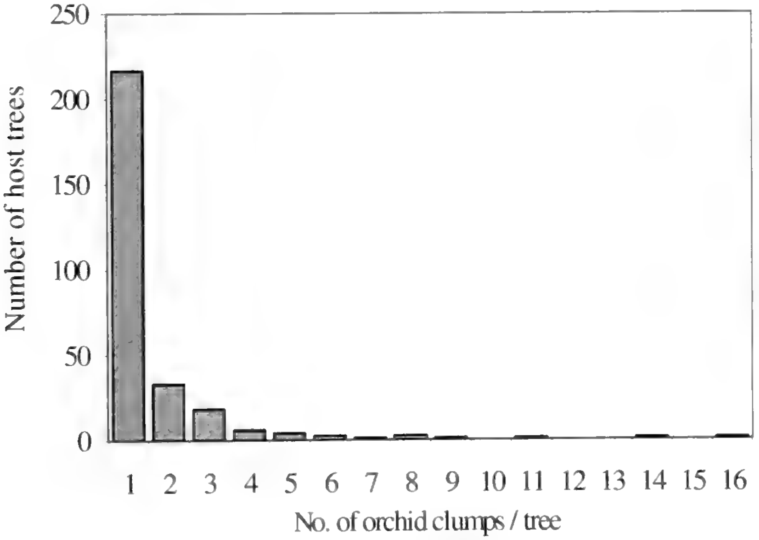

Fig. 2. Distribution of number of epiphytic orchid clumps per tree among the phorophyte trees.

clump. Only seven trees had more than seven clumps, and the maximum number of clumps recorded on a single phorophyte was 16.

Phorophyte diversity

A wide diversity of phorophyte species were colonised by epiphytic orchids. Both native (51 species) and exotic (6 species) phorophyte trees were recorded and phorophytes can be either evergreen (35 species) or deciduous (15 species) or semi-evergreen (5 species) but orchid density on evergreen phorophyte species was greater than deciduous (t=2.12, df=16, P=0.008 for quadrats, and t=2.01, df=48, P=0.05 for 72 sites). Orchids were found on 287 phorophytes of 57 different species (Fig. 3). A total of 30 different phorophyte species were recorded only once. The most frequently encountered phorophytes were *Mangifera indica* (49 trees) followed by *Artocarpus heterophyllus, Syzygium grandis, Tectona grandis* and *Lagerstroemia speciosa.*

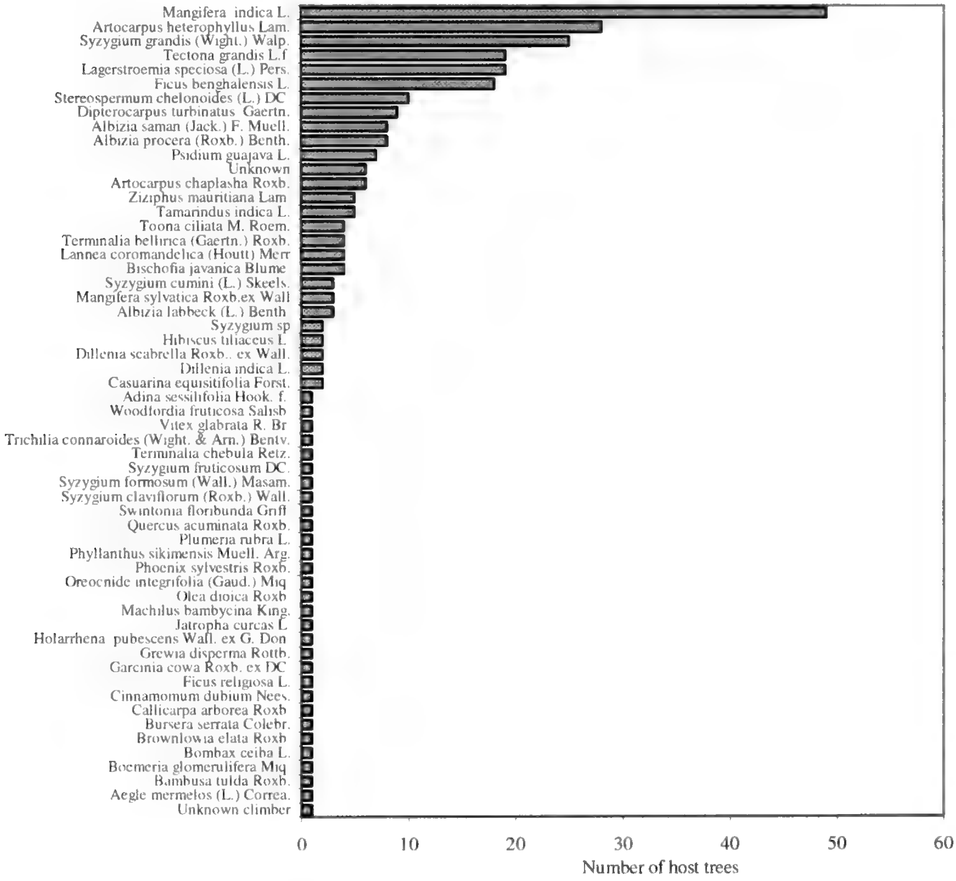

Fig. 3. Number of orchid-bearing trees per phorophyte tree species, ranked by abundance.

Orchid colonisation and phorophyte specificity

Number of orchid species and phorophyte tree density were positively correlated (r=0.902, df=55, P<0.001). A scatter plot of this data with 99% confidence intervals showed that the diversity of epiphytic orchids on the majority of phorophyte species was within expectation of the frequency of occurrence of the phorophyte (Fig. 4). Three native species *Syzygium cumini*, *Stereospermum cheolonoides* and *Syzygium grandis* had a wider diversity of orchids on them than expected indicating heterogeneity. No phorophyte species had lower levels of heterogeneity indicating an absence of phorophyte specificity. There was no indication of a levelling off in the relationship between phorophyte tree density and orchid diversity, indicating that saturation point had not been reached.

Colonisation pattern

The total number of orchid clumps recorded on an individual phorophyte species was correlated with the number of phorophytes of that species (r=0.944, df=55, P<0.001). Two phorophyte species, *Albizia procera* and *Albizia saman* supported more clumps than expected (Fig. 5) indicating increased suitability as phorophytes. The greatest number of clumps was recorded on *Mangifera indica*.

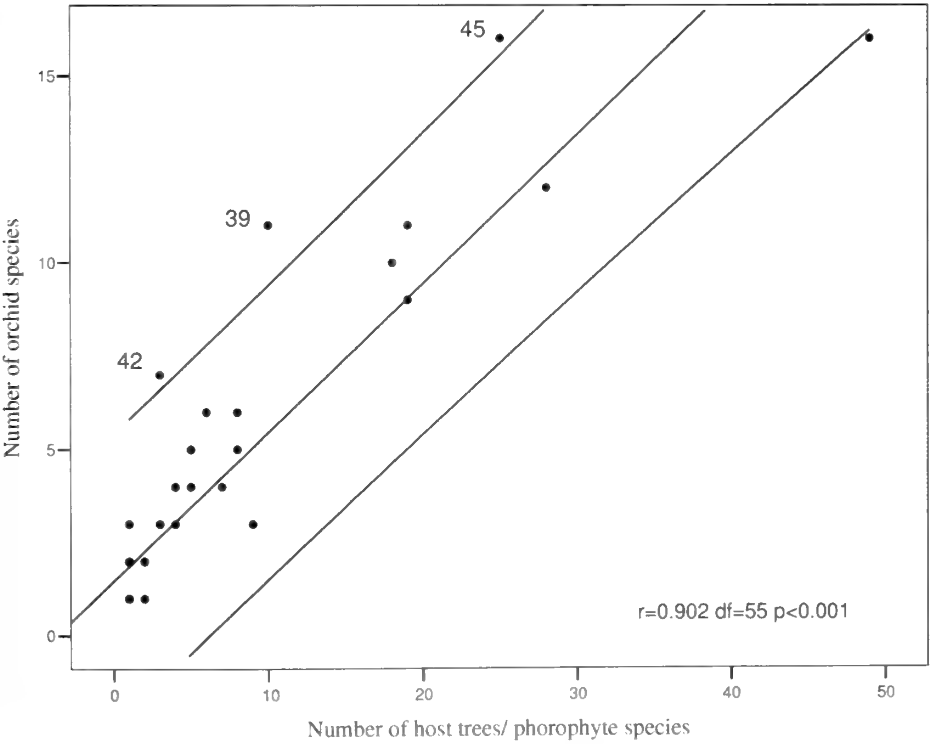

Fig. 4. The relationship between number of orchid species and phorophyte tree density. The regression line is fitted with 99% confidence intervals; 39: *Stereospermum chelonoides*, 42: *Syzygium cumini*, 45: *Syzygium grandis*.

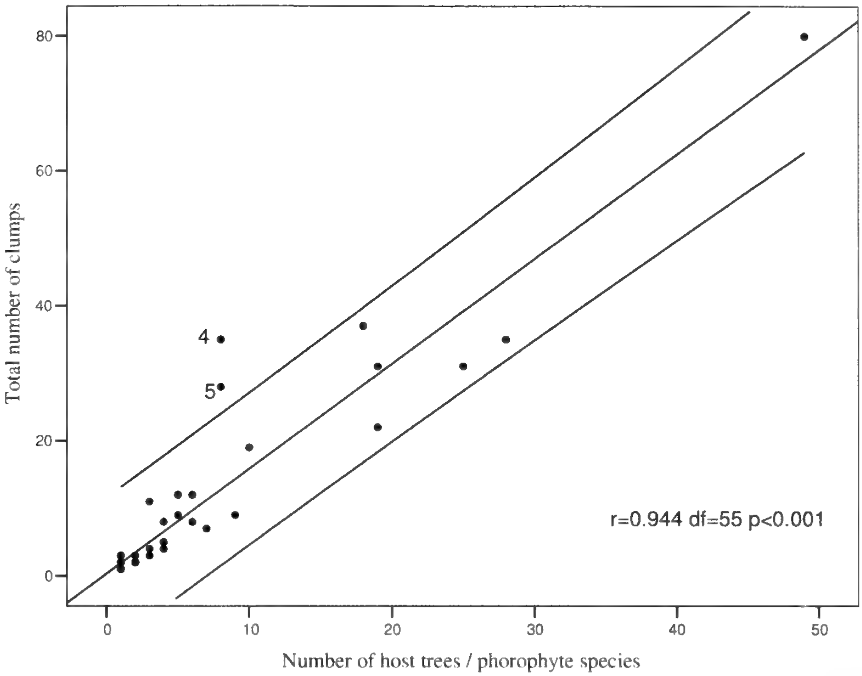

Fig. 5. The relationship between total number of epiphytic orchid clumps found and phorophyte tree density. The regression line is fitted with 99% confidence intervals; 4: *Albizia procera*, 5: *Albizia saman*.

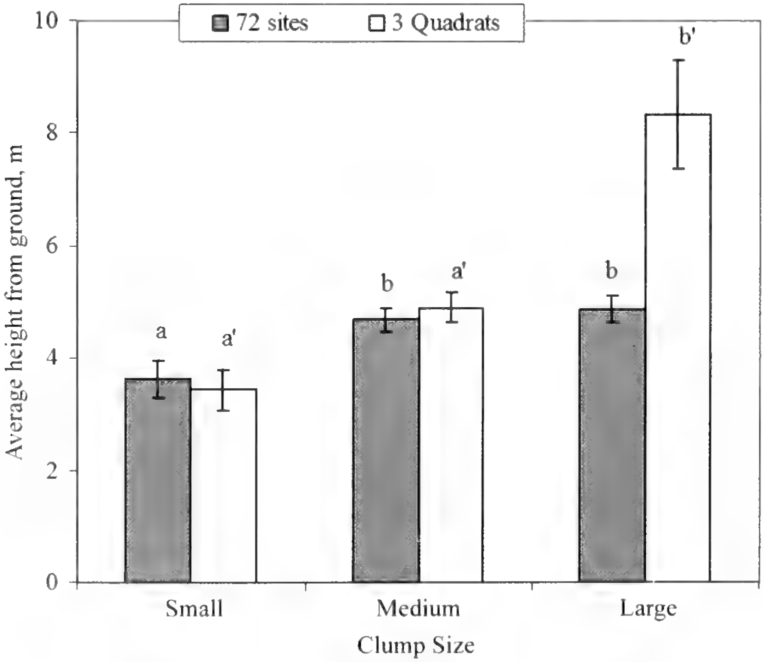

Fig. 6. Relative distribution of small, medium and large orchid clumps at different heights from the ground (mean+ SE).

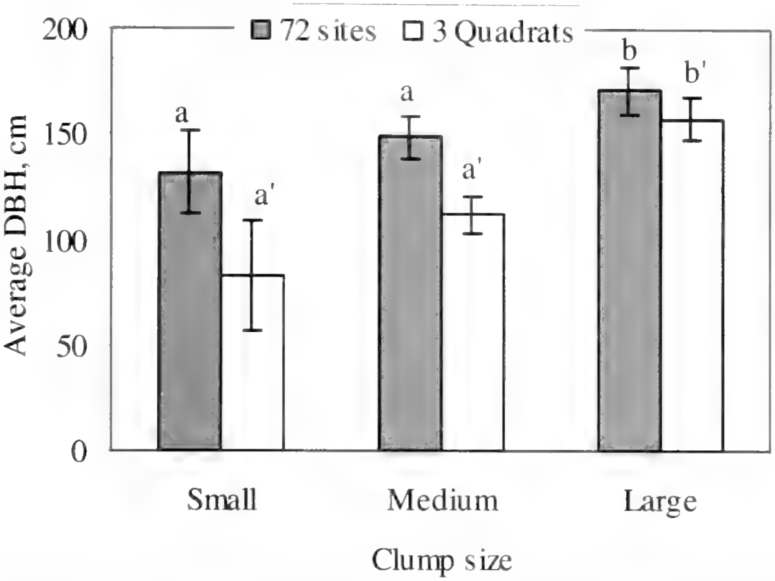

Fig. 7. Relative distribution of small, medium and large orchid clumps on phorophyte trees of different dbh sizes (Mean+SE).

The average height of occurrence of orchid clumps of different sizes is shown in Fig. 6. Small clumps are found at lower heights than medium or large clumps of epiphytic orchids (*F*=5.637, *df*=314, *P*=0.004; LSD and Tukey test showed significant differences between small and medium + large) in the 72 sites, and also at lower heights in the forest quadrats compared with large clumps (*F*=8.353, *df*= 41, *P*=0.001; LSD and Tukey test showed significant differences between large and small + medium clumps).

Clump sizes and average dbh of phorophytes were not significantly different among the 72 sites (*F*=2.143, *df*= 226, *P*=0.12) but in the forest quadrats the dbh of trees with large clumps was significantly higher than those for smaller and medium clumps (*F*=8.389, *df*=38, *P*=0.001; LSD and Tukey test showed difference between large and small; Fig. 7).

Colonisation of orchids in disturbed and undisturbed forest quadrats

Colonisation of trees by epiphytic orchids, phorophyte characteristics and area orchid diversity for the three forest quadrats were studied. A test of association between orchid presence on phorophytes and forest quadrats showed that orchids occur more frequently on trees in the quadrat sited in the more orchid-rich district than those from a quadrat in an area of lower orchid diversity (χ^2 =11.43, *df*=2, *P*=0.003; Fig. 8).

Within the forest quadrats, average dbh was associated with orchid occurrence (3×2 contingency table for large, medium and small dbh of trees with orchid presence, χ^2 =6.04, *df*=2, *P*=0.049). There was an association between clump size (large, medium and small) and forest quadrats (χ^2 =7.41 *df*=2, *P*=0.0246) indicating that more large clumps were found on trees at Sitapahar than expected (Fig. 9).

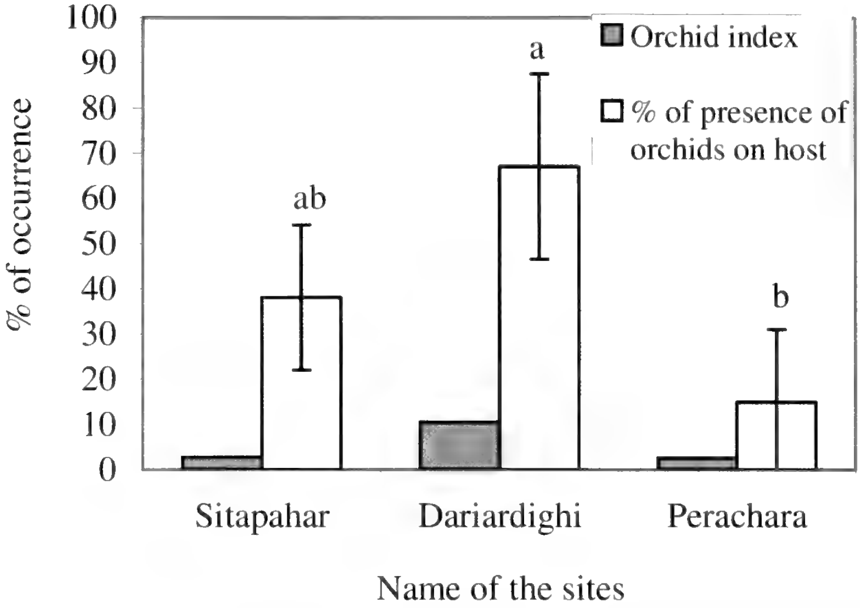

Fig. 8. The orchid diversity index and relative commonness of orchids on phorophyte trees, compared for the three 1-ha quadrat study sites; the latter with 95% confidence intervals shown.

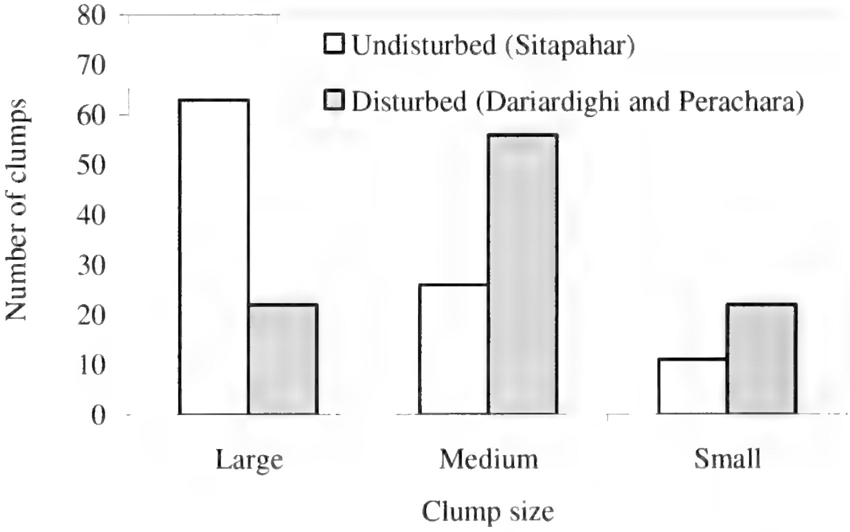

Fig. 9. Clump sizes of epiphytic orchids in the two different forest types.

Orchid colonisation in each of the forest quadrats follows the Poisson distribution (Table 2) indicating that Orchid colonisation is a rare and random event and one epiphytic orchid species does not attract or repel others on that phorophyte.

Table 2. Distribution of orchid clumps on trees above 5 m in height in 3 hectare forest quadrats and the χ^2 values obtained from a test of goodness of fit to values based on a Poisson distribution.

Places	Trees with no orchids	1 clump	2 clump	3 clump	4 clump	χ^2 values	df	P -values
Sitapahar	22	10	3	1	0	0.22	2	0.9
Dariardighi	7	10	3	0	1	1.09	3	0.78
Perachara	17	3	0	0	0	0.02	1	0.89
Total	46	23	6	3	1	0.47	3	0.93

Discussion

Epiphytic orchid diversity and distribution on phorophytes

The total number of epiphytic orchid species recorded during this project accounted for 39% of the total epiphytic orchid flora of Bangladesh. But considering the size of the study area (15% of Bangladesh), the epiphytic orchid species diversity of south-east Bangladesh is therefore reasonably diverse. In India, 14 epiphytic orchid species have been recorded from a tropical evergreen forest at Varagalaiar, Western Ghats (Annaselvam & Parthasarathy, 2001) and 26 species from a moist lowland forest of Eastern Himalaya (Padmawanthe et al. 2004). A total of 101 epiphytic orchid species were recorded from West Africa rain forest (Johansson 1974), 41 epiphytic orchid species from South Africa (Harrison 1972), 11 from a forest watershed of Puerto Rico (Migenis & Ackerman 1993), 232 from West Tropical Africa (Hepper 1968) and 414 from Zaire (Nihoul et al. 1969). The epiphytic orchid species diversity in south-east Bangladesh therefore appears to be only moderately rich in comparison with these other forest areas.

Orchids were found infrequently on trees throughout the 72 sites with the majority of species present in only one clump per phorophyte. A maximum of 16 clumps was found on an old tree of *Ficus benghalensis*. Thirty-six of the 41 epiphytic orchid species were found on less than 14 phorophytes. Epiphytic orchid occurrences on trees in south-east Bangladesh are therefore infrequent or rare and most do not form tree populations of more than one clump.

Phorophyte diversity

Most studies of epiphytes have concentrated on the epiphytes themselves and not on the phorophytes that support them. We have documented all the phorophytes for the epiphytic orchids in this study, together with a record of some of their characteristics. The 41 species of epiphytic orchids were found on 57 different phorophyte species of wide taxonomic diversity. The epiphytic orchids were found on both shrubby and small trees as well as very large trees, bamboos and date palms. The two most frequently encountered phorophytes were *Mangifera indica* (Mango) and *Artocarpus* *heterophyllus* (Jackfruit) and we found 16 and 12 different species of orchids on them, respectively. These phorophytes are very common, especially near to forest villages, as tree poachers do not cut these fruit-bearing trees.

Most of the epiphytic orchids were found on evergreen rather than deciduous tree species. However, further examination of this discrepancy in the forest quadrat showed no association between leaf persistency and orchid presence on the trees, indicating that there is no preference for one type of tree. Nevertheless epiphytic orchid density was greater in evergreen species than in deciduous ones, indicating that leaf persistence may influence secondary colonisation. This might result from the continuous presence of moisture throughout the year promoting seedling growth and/or shade effects, which maintain the growth environment and microclimate. Large openings in the canopy have been shown to reduce the abundance, distribution and diversity of shade-requiring epiphytes (Hietz 1999). Conversely, Annaselvam & Parthasarathy (2001) found that epiphyte density was greater on deciduous species in India than on evergreens. Architecture may play a critical role in determining phorophyte suitability (Migenis & Ackerman 1993).

Most individual phorophytes bore only one epiphytic orchid species on them. This agrees with Annaselvam & Parthasarathy (2001) who showed that most phorophytes supported only a single epiphyte on them. Benavides et al. (2005) found one phorophyte carried an average of 2.2 epiphytic individuals and 1.8 epiphytic species in the rain forests of Colombian Amazonia.

Phorophyte specificity and heterogeneity

No phorophyte specificity was found in the present study. Increase in the number of phorophytes of a single species was correlated with numbers of native species and exotic trees in line with expectation. Further, low levels of occurrence of epiphytic orchid species per native phorophyte supported the lack of specificity. Although *Thrixspermum trichoglottis* occurred most frequently on an exotic, *Psidium guajava,* this species also occurred on three native species. Orchids also showed no phorophyte specificity in the Bisley watershed (Migenis & Ackerman 1993). However, epiphytes often exhibit a certain degree of phorophyte preference, often on trees shared by co-occurring epiphytes, indicating the suitability of a tree for epiphyte colonisation (Benzing 1990). Phorophytic preference is also a common phenomenon in Puerto Rico and elsewhere in the Neotropics, but specificity is not common (Ackerman et al. 1989, Allen 1959, Zimmerman & Olmsted 1992). Phorophyte specificity has been shown, or at least surmised, for some Indonesian, Philippine and Puerto Rican orchids (Went 1940, Sanford 1974, Tremblay et al. 1998) but as in many other tropical forests (Johansson 1974, Todzia 1986, Zimmerman & Olmsted 1992) there was no evidence of phorophyte specificity exhibited by orchids in the present study.

There was also no indication of a levelling off of the relationship between phorophyte frequency and orchid diversity, suggesting that no species saturation had been reached. The total number of orchid clumps found on most phorophyte species increased with more records of the host in line with expectation. Two species of *Albizia procera* and *Albizia saman* supported more clumps than expected, indicating some preference for, or ease of, colonisation. These results are similar to those of Zimmerman & Olmsted (1992) who showed that commoner phorophytes bore more epiphytic species.

Colonisation pattern

Our data show that large clumps were found at greater height on the phorophytes, which might be expected as orchids age and increase in clump size with the growing tree. However, it might indicate habitat preferences for different epiphytic orchids within the phorophyte. No similar data directly match our findings due to lack of previous work on epiphyte clump size. Werneck & Espirito-Santo (2002) reported a higher abundance of epiphytes at intermediate heights on the phorophytes, but different epiphytic species showed very contrasting vertical distributions. Benavides et al. (2005) reported that epiphytic diversity was highest in the branches of crowns and lowest on the stem bases.

Werneck & Espirito-Santo (2002) found that epiphytic species differed significantly in their distribution along branch diameters of the phorophyte and our data showed that larger clumps were found more frequently on trees with larger dbh in the forest quadrats. Orchids tend to be restricted to larger phorophytes because of their preference for larger diameter supports (Zimmerman & Olmsted 1992). Prosperi (1998) also found a highly significant positive correlation between the rate of colonisation and host diameter above 50 cm, and according to Flores-Palacios & Garcia-Franco (2006) epiphytic communities are unsaturated, as the number of species increases with tree size and do not reach a ceiling in Guyana.

Colonisation of orchids in disturbed and undisturbed forests

Our data illustrate that forests in areas of richer epiphytic orchid diversity can have higher colonisation rates (even though disturbed) than forests in orchid-poor areas, even when undisturbed. This suggests that epiphytic orchid-rich areas therefore provide potential recruitment for all types of forests within that zone. However, our data suggest that throughout all forest types orchid colonisation is a random and rare event, with no attraction or repulsion shown by the presence of a single clump on a tree. Larger trees within the forests accumulate more epiphytic orchids and more large clumps, and undisturbed forests also have larger clumps. Our data suggest that logging of the most mature trees in a forest selectively modify the epiphytic orchid flora by combining the decimation of both the largest clumps of orchids, and the trees with the greatest colonisation, which may have accumulated over many years of growth.

The occurrence of epiphytic orchids tends to be biased towards the larger phorophytes, a pattern to be expected if large trees are more likely to accumulate epiphytes, as a result of increased branch area or increased time available for epiphytic colonisation (Zimmerman & Olmsted 1992). The rate of illegal felling of large trees has probably already drastically affected the epiphytic orchid flora.

The data presented here show that the diversity of epiphytic orchids is now based on a fragile phorophyte system because most orchids occur only singly on a tree. In addition, a large number of epiphytic orchid species have been found only once (30%). So, careful management is essential to conserve the larger phorophytes as well as the epiphytic orchids, otherwise one third of all the epiphytic orchids will experience severe decline.

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Habitat and ecological preferences of *Hydriastele costata* (Palmae) in Waigeo Island, West Papua

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ABSTRACT. The research was conducted to test hypotheses about the significance and influence of edaphic parameters and association patterns in governing the occurrence and abundance of the karst palm *Hydriastele costata* and its co-occurrence with other plant species in Waigeo Island, West Papua. The results indicate that a number of interrelating edaphic factors influence the palm's occurrence and abundance. The palm showed a preference for dry, well-drained soil, with high magnesium (Mg^{2+}) content. Most colonies occurred in localities where Mg^{2+} content was very high. High alkaline concentrations also strongly corresponded to the presence of the emergent palm. Six of 15 tropical plant species were positively associated while the rest were negatively associated with *H. costata*. Four species (*Casuarina rumphiana*, *Decaspermum bracteatum*, *Baeckea frutescens*, and *Pinanga rumphiana* were strongly associated with *H. costata*, as indicated by their high association degrees using the Ochiai indices. The palm *P. rumphiana* appears to have similar habitat requirements as *H. costata*. The xerophytic palm *H. costata* tended to occupy sites with medium carbon nitrogen (C/N) ratios where all sampled populations occurred in habitats with average C/N values more than 10. Based on the *r*-squared values, exchangeable Mg^{2+} and calcium (Ca^{2+}) appeared to have more influence on plant density and frequency than on crown and basal areas. The exchangeable Ca^{2+} contents showed a similar pattern to Mg^{2+} concentrations. Curiously, potassium (K^+), sodium (Na^+), aluminium (Al^{3+}) and hydrogen (H^+) contents did not show significant relationships with the palm abundance parameters.

Keywords. Association, co-occurrence, habitat preferences, *Hydriastele costata*, palms, Waigeo, West Papua

Introduction

Understanding the mechanisms for species co-occurrence and habitat preference (specialisation) is crucial for habitat management (Begon et al. 1996, Ludwig & Reynolds 1988, Mohler 1990, Nakashizuka 2001, Christie & Armesto 2003, van der Heijden et al. 2003, Hall et al. 2004). Although the detection of co-occurrence or association among or between species and environmental variables does not provide a causal understanding (Morisita 1959, Schluter 1984, Silvertown et al. 1992, Real & Vargas 1996), it can be used to generate hypotheses of possible underlying causal factors.

Palms often show local or regional patterns of co-occurrence and ecological preferences (Tomlinson 1979, House 1984, Kahn & Mejia 1990, Moraes 1996, Svenning 1999). Some palms appear to be adapted to specific edaphic conditions, such as soil quality, drainage and type (House 1984, Tomlinson 1990, Moraes 1996, Widyatmoko & Burgman 2006). Most tropical rain forest tree species have strongly aggregated spatial distribution patterns due to a high degree of habitat specialisation (Ashton 1998, Phillips 1998, Condit et al. 2000, Hubbell 2001). However, Duivenvoorden (1995, 1996) argued that most trees of the well-drained upland habitat in Colombian Amazonia are likely to be soil generalists rather than specialists, implying limited importance of microhabitat specialisation for maintaining tree species richness.

There has been a lack of consensus about the importance of the correlations between plant abundance and edaphic conditions at local and intermediate spatial scales, e.g., at 1–100 km^2 (Gartlan et al. 1986; Swaine 1996; Clark et al. 1998, 1999; Hall et al. 2004). Tropical soils are not homogeneous at regional, intermediate or even local scales (Richter & Babbar 1991, Hall et al. 2004) and abrupt discontinuities in edaphic conditions are common features (Clark et al. 1998). Regional or intermediate spatial scales refer to strong environmental discontinuities (habitat types) while local spatial scales refer to environmental conditions that vary at scales less than 10^3 m, such as treefall gaps and local topographic variation (Svenning 1999).

Plant co-occurrence and abundance may be determined largely by nutrient availability, heterogeneity of the biotic and abiotic environment, and microhabitat specialisation (Silvertown & Law 1987, Ludwig & Reynolds 1988, Kahn & Mejia 1990, Hatfield et al. 1996, Clark et al. 1998, Svenning 1999, Webb & Peart 2000, van der Heijden et al. 2003, Palmiotto et al. 2004). Some other studies have shown that tropical plant species distributions and community composition are correlated with soil nutrient status (Tucker 1992, Poulsen 1996, Clark et al. 1998, Svenning 2001, Widyatmoko 2001, Widyatmoko & Burgman 2006, Widyatmoko et al. 2007) such as magnesium and phosphor (Olsen & Sommers 1982, Vitousek & Sanford 1986, Baillie et al. 1987, Suarez 1996, Sollins 1998, Tiessen 1998, Potts et al. 2002, Hall et al. 2004, Palmiotto et al. 2004) as well as calcium, potassium, and sodium contents (Suarez 1996, Widyatmoko & Burgman 2006).

Spatial distribution patterns may also be determined by complex relationships within and between species, including seed dispersal (Bell 2000), competition for pollinators (Armbruster 1995, Svenning 1999), recruitment and regeneration (Harms et al. 2000, Christie & Armesto 2003, Widyatmoko et al. 2005), density dependence (Webb & Peart 2000), intermediate disturbance (Molino & Sabatier 2001) or variation in topography and soil water (Campbell 1985, Swaine 1996, Davie & Sumardja 1997, Clark et al. 1998, Svenning 2001). Very little information is available about the roles and influences of soil conditions and biotic associations on plant abundance and co-occurrence (Higgs & Usher 1980, House 1984, Gentry 1988, Duivenvoorden 1995).

Hypotheses regarding species co-occurrence invoke equilibrium and non-equilibrium explanations (Svenning 1999, Nakashizuka 2001, Groeneveld et al. 2002, Edmunds et al. 2003). Equilibrium hypotheses assume that species co-occur by occupying different niches (niche partitioning), while non-equilibrium hypotheses emphasise local fluctuations, disturbance and chance events that do not determine species composition, although they may result in expectations for relative species abundances (Hubbell 2001, Chisholm & Burgman 2004). Both equilibrium and non-equilibrium processes seem likely to contribute to the composition of most plant communities (Nakashizuka 2001).

The interspecific association test is a simple species-based approach for preliminarily defining community types that can be recognised by a small assemblage of common species. If sets of species are found to co-occur, and the occurrence of these sets can be related to habitat factors, such information will provide more compelling evidence for niche processes structuring the community than does a single species approach.

The objective of this research was to (1) test hypotheses about the significance and influence of edaphic parameters in governing the occurrence and abundance of the important karst palm *Hydriastele costata* F.M.Bailey in a tropical lowland rain forest of Waigeo Island, West Papua, and (2) assess the tendency of the palm to co-occur with other plant species. We addressed three questions to answer. First, do local edaphic conditions in different habitat types affect the occurrence and abundance of *H. costata*? Second, does the palm species associate with other plant species in the Waigeo forest? Third, if so, how strong is the association? Such information is required to support the reserve management system, particularly through long-term monitoring of significant populations of the species occurring on different habitat types. Long-term monitoring programs will provide foundations for developing management prescriptions and conservation priorities for the valuable species and its habitat.

Materials and methods

Study species

Hydriastele costata (Arecaceae) is a solitary, erect, straight, unarmed, tall (up to 20–30 m), pleonanthic, monoecious palm species (Uhl & Dransfield 1987, Widyatmoko et al. 2007). The palm species occurs in New Guinea, Bismarck Archipelago and northern Australia, particularly in the humid lowland and hill tropical rain forests at altitudes from 0 up to 500 m above sea level, occupying mainly the forest upper canopy, preferring coastal calcareous soils. *H. costata* is not only of interest from an ecological point of view, but also in terms of economic significance since it provides a number of benefits. The palm is used as an ornamental plant, the stem is used for constructing local houses (floors and laths), while the hard outer part of the stem is locally used for making spears.

Study sites

The study focused on the Waifoi Forest and Kamtabae River located within the East Waigeo Nature Reserve, the Raja Ampat Islands, West Papua (Fig. 1), at altitudes ranging from 0 to 500 m above sea level, where *H. costata* mostly occurs. The camp established at Kamtabae River (130°43'38.2"E 0°5'53.3"S) was used as the reference

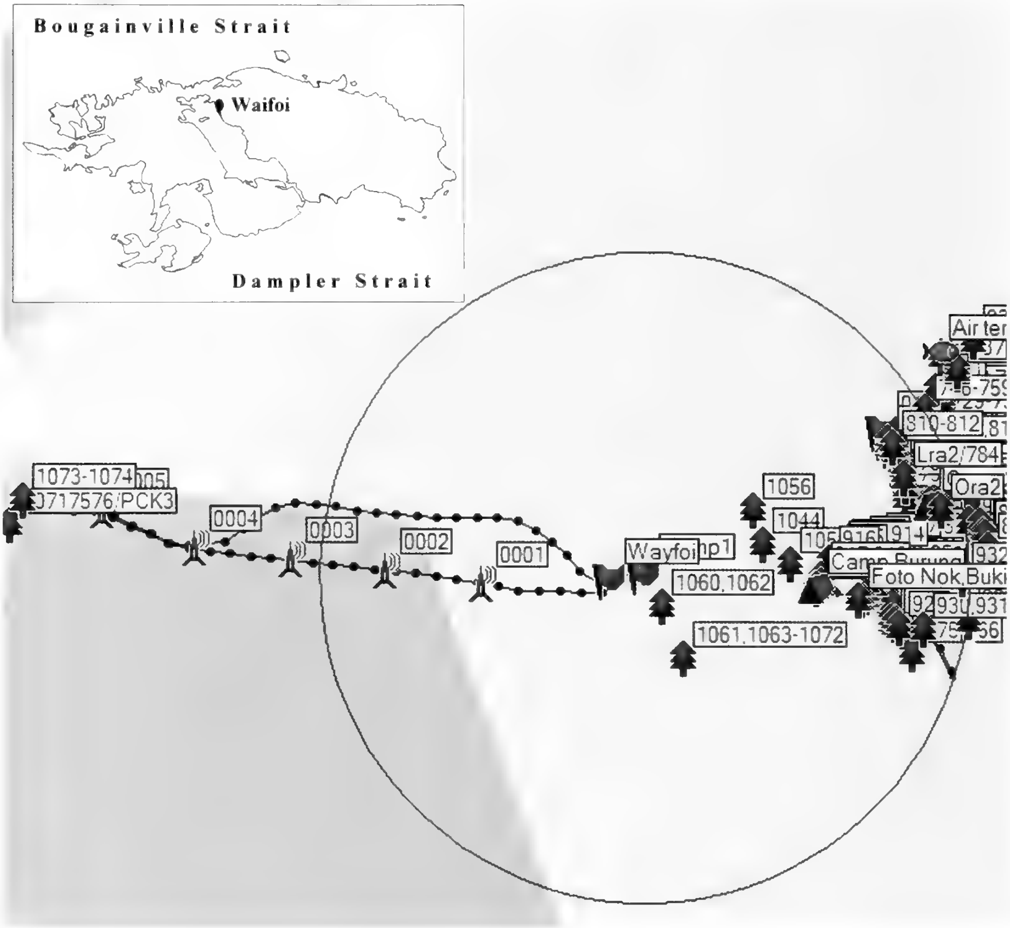

Fig. 1. The study area where coordinates and elevation of all sites studied (tree symbols) were recorded; Waifoi (Wayfoi) village is at the center of the circle. Inset shows locality of Waifoi on Waigeo.

point to explore the surrounding forests. Different directions comprising all four aspects were covered in order to comprehensively cover the study area. Lowland and hill forests of mixed-age indigenous vegetation, with slopes ranging from 30 to 70%, dominated the inland nature reserve topography.

East Waigeo Nature Reserve was established in 1996 based on the decree of the Indonesian Minister of Forestry No. 251/Kpts-II/1996 covering a total area of 119,000 hectares, located between 130°39'49"E and 130°55'54"E and between 0°02'27"S and 0°08'51"S. It has the 'Af' climate type, experiencing eight consecutive wet months. All months have an average temperature above 18°C (ranging from 23°C to 32°C). Waigeo only has small seasonal temperature variations of less than 3°C (the Koppen's System, Tarbuck & Lutgens 2004); with an average humidity of 85% during June 2007.

Waigeo Island is one of the four major islands of the Raja Ampat Archipelago. The waters and environment around Waigeo Island have been known as the most biodiverse marine area in the world, especially in terms of coral reefs and fish species (Webb 2005, Pemerintah Kabupaten Raja Ampat & Conservation International Indonesia 2006). However, despite it being a biologically very rich area, little is known about the Islands' plant diversity and terrestrial resources (Badan Perencanaan Pembangunan Nasional - Bappenas 2003, Webb 2005). Detailed surveys focusing on the plant diversity will provide important baseline data for managing and conserving the Islands' biodiversity sustainably (Webb 2005).

Geologically, Waigeo Island is interesting, in having extensive karst ecosystems, alluvium substrates, acid volcanic and ultrabasic rocks, with some relatively high mountains (Jepson & Whittaker 2002, Webb 2005, Pemerintah Kabupaten Raja Ampat & Conservation International Indonesia 2006). The flora must be diverse according to the substrate and biogeographic reasons, as well as habitat characteristics which range from submontane forests to sago swamps and mangroves (via forests on karst and acid volcanics). Hill forests on volcanic substrates and karst formations extensively occur on this island. The island ultrabasic scrub is also unique and widely known for its endemic species (Webb 2005). Each island of the Raja Ampat has its own characteristics, especially in terms of vegetation composition and habitat types. Waigeo Island is botanically very important and valuable, despite its relatively small size compared to the main island of Papua (Johns 1995, Johns 1997, CI 1999).

Selection of habitat types

In order to study *H. costata* habitat preferences, eight habitat types were selected: coastal line (seashore), coastal hill slope, coastal hill top, inland river bank, inland hill slope, inland hill top, disturbed forest (most native species present), and converted forest (most native species removed). The characteristics of each habitat type (including slope, soil formation, elevation soil pH, average humidity, and average temperature) were described and recorded.

Vegetation structure and composition

A series of 24 belt transects (of 100 m × 10 m each) was established at the eight habitat types selected (i.e., three transects on each habitat), stretching from the camp at the Kamtabae River (130 43'38.2"E 0 5'53.3"S) to behind the Waifoi Village (130°42'46.7"E 0°6'5.9"S). Locations of each habitat type and belt transect were recorded using a Garmin Global Positioning System MAP 175. The major axes of all transects were orientated north-south derived from a selected compass bearing (Krebs 1989, Cropper 1993). All stemmed individuals of *H. costata* within each transect were counted. Damaged or dead individuals were not included. Land slopes were measured using a clinometer (SUUNTO Optical Reading Clinometer PM-5), while soil pH and humidity were measured using a soil tester Demetra patent no. 193478 Electrode Measuring System. Soil profiles were sampled by using a soil sampler the Belgium auger 1 m. Soil analyses were conducted at the Soil Research Center, Bogor. The level of forest (habitat) disturbance was determined on the basis of the proportion of the remaining native species.

Interspecific association (co-occurrence)
Association patterns among co-occurring species were tested using the chi-square test statistic by constructing the hypothesis that two species are not associated at some predetermined probability level. Fifteen plant species were tested for association from 67 observed. The strength of each association was tested using the Ochiai Index (OI) as recommended by Ludwig & Reynolds (1988):

$$\mathrm{OI} = \frac{a}{\sqrt{a+b}\,\sqrt{a+b}}$$

Where:
a = the number of plots where both species (*H. costata* and the paired species) occur;
b = the number of plots where *H. costata* occurs, but not the paired species; and
c = the number of plots where the paired species occurs, but not *H. costata*.

Test of association. The palm was absent from one of the eight observed habitat types. The site was in the Waifoi village and was regarded as non-natural forest area (i.e., the coexisting plants have been planted with *Theobroma cacao*). Measures of interspecific association were based on the presence and absence of species within quadrats developed. A total of 144 quadrats of 5 m × 5 m each were sampled from the observed sites within the reserve with different vegetation types and associations. Quadrats were arranged systematically in an alternating pattern within the belt transects (of 100 m × 10 m each) in order to cover uniformly both sides of the axes (Mueller-Dombois & Ellenberg 1974, Cox 1974, Sokal & Rohlf 1981, Ludwig & Reynolds 1988). The data were then summarised in the form of a 2 × 2 contingency table.

The null hypothesis (H_0) constructed was that the distribution of *H. costata* is independent of the other species. To test the null hypothesis of independence, the chi-square test statistic (χ_t) was used (Ludwig & Reynolds 1988). The significance of the chi-square test statistic is determined by comparison with the chi-square distribution (χ_d) for 1 df at $\alpha = 0.05$. If $\chi_t > \chi_d$ the null hypothesis is rejected. Rejecting the null hypothesis indicates an association between *H. costata* and the paired species, implying that the two species co-occur at a frequency greater than expected by random association. Positive or negative associations were determined by comparing the value of observed occurrences ($O_{(a)}$) to that of expected occurrences ($E_{(a)}$). If observed is greater than expected, there is a positive association (the pair of species occurred together more often than expected if independent).

Measure of the strength of association. The Ochiai Index (a measure of association) was used to quantify the strength of association between the species tested (i.e., *H. costata* and the paired species), as the association test can only determine whether the species tested are associated or not associated, but not the degree of the association. The index was recommended by Janson & Vegelius (1981) and Hubalek (1982) as it proved less biased. The value of the Ochiai Index is equal to 0 at no association and 1 at complete or maximum association.

Results

Habitat preferences

H. costata seemed to prefer specific habitat types. Highest densities occurred on hill slopes and tops near the coastal area (Table 1, Fig. 2). In contrast, the palm was suppressed at the shore and even absent from converted forest where most native species have been removed and replaced by *Theobroma cacao* (Fig. 2). Although the palm tolerated minor forest disturbance, the populations were generally low in this type of habitat, indicating a tolerance of sub-optimal conditions. The highest density was found on ultrabasic soil, on steep slopes and dry-open canopy gaps, where there were 72.4 adult individuals ha^{-1} (Table 1).

Species co-occurrence

Sixty seven possible co-occurring species were analysed, of which 15 species were tested for association with *H. costata*. Six of these 15 tested species were positively associated while the rest were negatively associated (Table 2). For the six species (*Casuarina rumphiana* Miq., *Decaspermum bracteatum* (Roxb.) A.J.Scott, *Baeckea frutescens* L., *Pinanga rumphiana* (Mart.) J.Dransf. & Govaerts, *Exocarpos latifolius* R.Br., and *Myrsine rawacensis* A.DC.), the association with *H. costata* was strong,

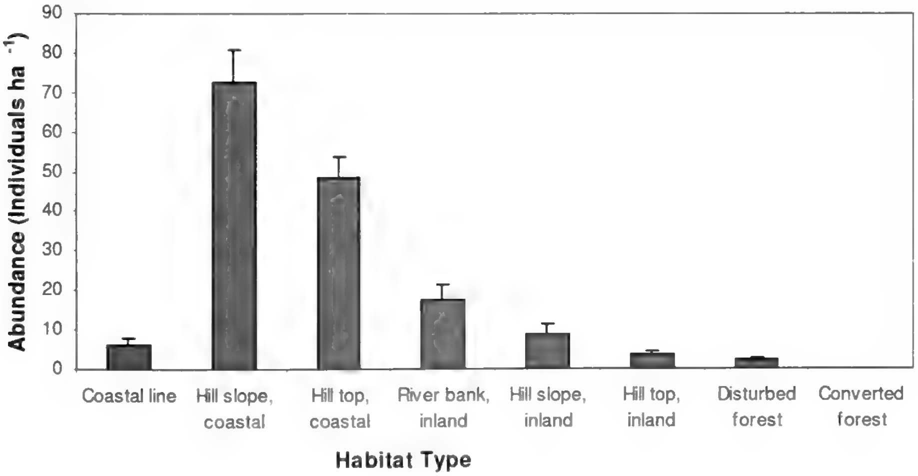

Fig. 2. Population densities of *Hydriastele costata* at different habitat types within the East Waigeo Nature Reserve, the Raja Ampat Islands, West Papua.

Table 1. The abundance of *H. costata* at various habitat types within the East Waigeo Nature Reserve, the Raja Ampat Islands, West Papua. Mean abundance ± S.D. (95% Confidence Interval).

Habitat type	Abundance (ha^{-1})	Habitat characteristics	Altitude (m asl)	Soil pH	Av. Humidity (%)	Av. Temp (°C)
Coastal line/shore	6.2 ± 1.6	0–30% slope, tidal influences, mud formation	0–10	6.2	82 ± 8.17	30.9
Hill slope, coastal	72.4 ± 5.4	30–80% slope, dry, open (wide canopy gaps), karst, ultrabasic soil	20–100	7.2	65 ± 7.02	31.9
Hill top, coastal	48.3 ± 5.3	30–60% slope, very dry, wide canopy gaps, karst, ultrabasic soil	100–150	7.2	63 ± 6.24	31.7
River bank, inland	17.5 ± 3.9	0–30% slope, lowland, alluvium, frequent floods	30–40	6.0-6.9	89 ± 8.29	28.5
Hill slope, inland	8.6 ± 2.9	30–70% slope, hill forest, alluvial deposit, volcanic soils	40–120	6.6–7.0	84 ± 6.72	28.3
Hill top, inland	3.4 ± 1.1	30–60% slope, hill forest, alluvial deposit	120–170	6.1–6.2	82 ± 9.02	27.6
Disturbed forest	2.2 ± 0.3	10–40%, most native species remained, *Lansium domesticum* planted	60–100	6.4–6.8	81 ± 6.48	29.1
Converted forest	0	10–40%, most native species removed, cacao planted	20–60	6.1–6.3	74 ± 6.01	29.6

indicated by their >0.5 indices. Although in some sites *Livistona brevifolia* Dowe & Mogea and *Licuala graminifolia* Heatubun & Barfod were found together with *H. costata*, their co-occurrence was not consistent. Surprisingly, the apparently closely associated species *Styphelia abnormis* (Sond.) F.Muell. and *Wendlandia buddlejacea* F.Muell. were negatively associated with *H. costata*. Unlike *Orania regalis* Blume ex Zipp., which is a shade-tolerance species, *H. costata* prefers and occupies karst and open coastal areas. As a consequence, their association degree was very low (Table 2).

A number of interrelating edaphic factors appeared to explain the occurrence

Table 2. Results of the association tests using the chi-square test statistic (χt) between *H. costata* and the fifteen co-occurring species. Values of the Ochiai Index are 0 at "no association" and 1 at "complete (maximum) association".

Paired species	Result of chi-square test	Types of Association	Strength of association (Ochiai Index)
Casuarina rumphiana	Associated	Positive	0.69
Decaspermum bracteatum	Associated	Positive	0.67
Baeckea frutescens	Associated	Positive	0.62
Pinanga rumphiana	Associated	Positive	0.61
Exocarpos latifolius	Associated	Positive	0.55
Myrsine rawacensis	Associated	Positive	0.52
Styphelia abnormis	Associated	Negative	0.43
Wendlandia buddlejacea	Associated	Negative	0.42
Ploiarium sessile	Associated	Negative	0.31
Livistona brevifolia	Associated	Negative	0.24
Decaspermum fruticosum	Associated	Negative	0.19
Licuala graminifolia	Associated	Negative	0.16
Pometia pinnata	Associated	Negative	0.15
Sommieria leucophylla	Associated	Negative	0.11
Orania regalis	Associated	Negative	0.07

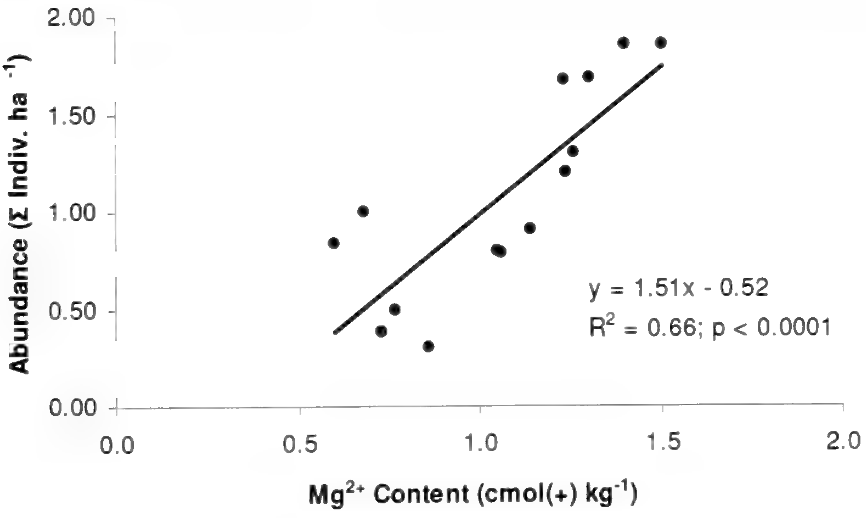

Fig. 3. Relationship between Mg^{2+} content and density of *Hydriastele costata* within the East Waigeo Nature Reserve, Waigeo. Mg^{2+} content values are Log_{10} and abundance values are Log_{10} individuals ha-1.

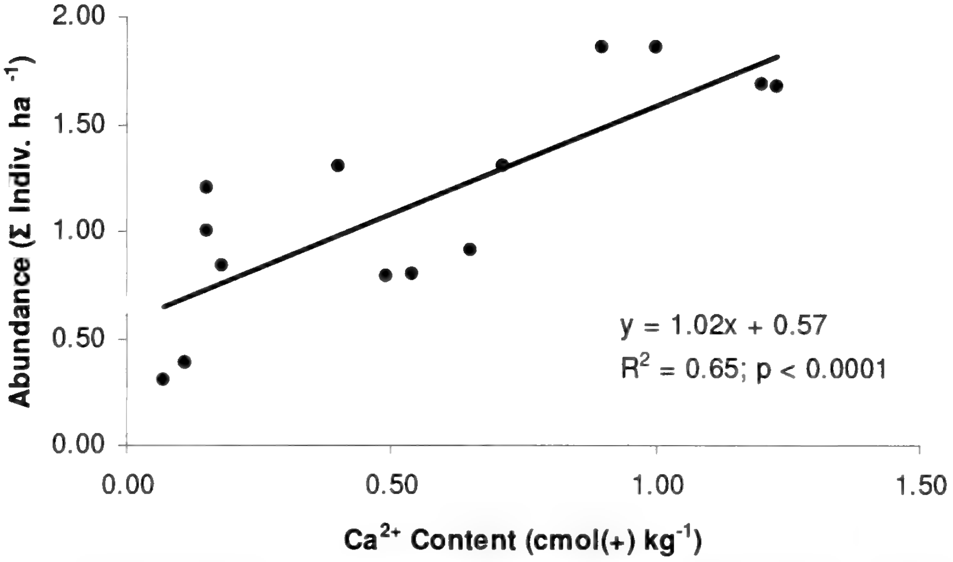

Fig. 4. Relationship between Ca^{2+} content and density of *H. costata* within the East Waigeo Nature Reserve, Waigeo. Ca^{2+} content values are Log_{10} and abundance values are Log_{10} individuals ha^{-1}.

Table 3. Results of the soil analyses conducted at six different habitat types within the East Waigeo Nature Reserve, Waigeo, West Papua. *Hill slope, coastal*: Horizon Ao (0–13 cm), A1 (13–48.5 cm), A2 (48.5–78.5 cm), AB (78.5–148 cm). *Hill top, coastal*: Horizon Ao (0–7 cm), A1 (7–18 cm), A2 (18–32.5 cm), AC (32.5–86.5 cm). *Hill slope, inland*: Horizon Ao (0–20 cm), A1 (20–40 cm), A2 (40–60 cm), AB (60–80 cm). *Hill top, inland*: Horizon Ao (0–15 cm), A1 (15–35 cm), A2 (35–75 cm). *River bank, inland*: Horizon Ao (0–16 cm), A1 (16–40 cm). *Coastal line*: Horizon Ao (0–10 cm).

Parameter	Hill slope, coastal				Hill top, coastal				Hill slope, inland				Hill top, inland			River bank, inland		Coastal line
	Ao	A1	A2	AB	Ao	A1	A2	AC	A0	A1	A2	AB	Ao	A1	A2	Ao	A1	Ao
pH	6.6	6.8	6.9	7.1	6.6	6.8	7.0	7.1	6.0	6.1	6.6	6.9	6.1	6.1	6.2	6.4	6.8	7.2
C/N	8	8	10	8	7	9	9	11	8	9	8	8	12	9	8	8	8	12
Ca2+	10	8.0	5.6	7.5	16	17	13	10	1.4	1.3	1.5	0.8	11.7	10.5	10.7	2.5	1.4	3.3
Mg2+	25	29	25	27	20	18	19	17	4.8	4.0	2.4	6.1	5.9	8.2	13.9	18.1	17.2	11.3
K+	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1
Na+	0.1	0.1	0.2	0.1	0.2	0.2	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.2	0.3	0.2	0.2	0.3
Al3+	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
H+	0.0	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.1	0.1	0.1

and abundance of *H. costata*. This palm showed a preference for ultrabasic soils, steep slopes, and dry-open canopy gaps, with high magnesium (Mg^{2+}) and calcium (Ca^{2+}) contents. The largest population occurred on hill slopes where the highest magnesium content was recorded (Table 3). There was a strongly positive correlation between the abundance of *H. costata* and the soil mineral Mg^{2+} content (Fig. 3). The three largest populations (coastal hill slopes, coastal hill tops, and inland river bank) occurred in sites where Mg^{2+} contents were high (Table 3). According to the Soil Research Center (1983), a Mg^{2+} content >8.0 cmol(+)/kg was categorised as "very high" (Table 4). To some extent, Ca^{2+} contents also influenced the occurrence of *H. costata*, i.e., higher concentrations of Ca^{2+} corresponded with higher densities of the palm (Fig. 4), although the trend was not as clear as that for Mg^{2+}. Curiously, K^+, Na^+, Al^{3+} and H^+ concentrations did not show significant relationships with *H. costata* abundance parameters. The palm tended to occur in sites with lower C/N ratios (higher N contents). All observed populations occurred in habitats with average C/N values <10.

Table 4. Classification and criteria for soil chemical properties as defined by the Soil Research Center (1983).

Soil Properties	Very Low	Low	Medium	High	Very High
C (%)	<1.00	1.00–2.00	2.01–3.00	3.01–5.00	>5.00
N (%)	<0.10	0.10–0.20	0.21–0.50	0.51–0.75	>0.75
C/N	<5	5–10	11–15	16–25	>25
P_2O_5 HCl (mg/100g)	<10	10–20	21–40	41–60	>60
P_2O_5 Bray 1 (ppm)	<10	10–15	16–25	26–35	>35
P_2O_5 Olsen (ppm)	<10	10–25	26–45	45–60	>60
K_2O HCl 25% (mg/100g)	<10	10–20	21–40	41–60	>60
Cation Exchange Capacity (cmol(+)/kg)	<5	5–16	17–24	25–40	>40
K^+ (cmol(+)/kg)	<0.1	0.1–0.2	0.3–0.5	0.6–1.0	>1.0
Na^+ (cmol(+)/kg)	<0.1	0.1–0.3	0.4-0.7	0.8–1.0	>1.0
Mg^{2+} (cmol(+)/kg)	<0.4	0.4–1.0	1.1–2	2.1–8.0	>8.0
Ca^{2+} (cmol(+)/kg)	<2	2–5	6–10	11–20	>20
Alkali Saturation (%)	<20	20–35	36–50	51–70	>70
Alumin. Saturation (%)	<10	10–20	21–30	31–60	>70
pH H_2O	<4.5 – 5.5 Acid	5.6 – 6.5 Slightly Acid	6.6 – 7.5 Neutral	7.6 – 8.5 Slightly Alkaline	>8.5 Alkaline

The largest colony at the coastal hill slopes had an average C/N value of 8.5, followed by the coastal hill tops colony with an average value of 9.0 (Table 3).

Based on the *r*-squared values, exchangeable Mg^{2+} appeared to have more influence on plant density and frequency than on basal area and crown area (Table 5). The exchangeable Ca^{2+} concentrations showed a very similar pattern to Mg^{2+} contents, while C/N values seemed to have a negative correlation with frequency and density (i.e., higher values of C/N correlated with lower plant densities). Soil pH appeared to have more influence on plant density than on plant frequency. On the other hand, K^+, Na^+, Al^{3+} and H^+ contents did not show significant relationships with the palm abundance parameters, as indicated by their low correlation coefficients (Table 5).

Discussion

The positive association of *H. costata* with high contents of Mg^{2+} and Ca^{2+} is similar to that of the Papuasian palm *Orania regalis* (Widyatmoko 2009), the Malayan rain forest bertam palm *Eugeissona triste* Griff. (Fong 1977) and the Amazonian palms *Phytelephas macrocarpa* Ruiz & Pav. and *Astrocaryum murumuru* Wallace var. *murumuru* (Vormisto 2002) which prefer higher soil mineral contents. On the other hand, the association pattern of *H. costata* is different from that of the lipstick palm *Cyrtostachys renda* Blume (Widyatmoko & Burgman 2006) and the bayas palms *Oncosperma horridum* Scheff. and *O. tigillarium* (Jack) Ridl. (House 1984) which prefer low levels of Ca^{2+}, Mg^{2+} and K^+. Widyatmoko & Burgman (2006) showed that *C. renda* preferred sandy, well-drained soils with low mineral contents, while House (1984) found that *O. horridum* and *O. tigillarum* did not avoid flooded areas and poorly drained clay substrates.

Table 5. Values of correlation coefficient (*r*-squared) between edaphic parameters and abundance of *H. costata* within the East Waigeo Nature Reserve, Waigeo. Notes: (+) indicates a positive correlation; (-) indicates a negative correlation; * $p < 0.0001$; sample size (n) = 14.

Edaphic Parameters	Frequency	Density (Σ Individuals ha^{-1})	Basal Area (m^2 ha^{-1})	Canopy Circle Area (m^2 ha^{-1})
pH	(-) 0.52	(+) 0.61*	(-) 0.31	(-) 0.30
C/N	(-) 0.60*	(-) 0.62*	(-) 0.27	(-) 0.31
Exch. Ca^{2+}	(+) 0.62*	(+) 0.65*	(+) 0.41	(+) 0.41
Exch. Mg^{2+}	(+) 0.63*	(+) 0.66*	(+) 0.54	(+) 0.47
Exch. K^+	(+) 0.32	(+) 0.38	(+) 0.33	(+) 0.29
Na^+	(+) 0.41	(+) 0.35	(+) 0.39	(+) 0.36
Al^{3+}	0.00	0.00	0.00	0.00
H^+	(-) 0.34	(-) 0.39	(-) 0.28	(-) 0.24

Unlike *Licuala graminifolia* which is a relatively shorter-lived opportunistic species that rapidly colonises canopy gaps, *H. costata* is a slower-growing, long-lived species constituting an emergent canopy layer. Unlike *H. costata*, *L. graminifolia* occupies lower subcanopies, thus having different levels of sunlight exposure. *Licuala graminifolia* is more widely distributed throughout Papua. To some extent, *H. costata*, *Pinanga rumphiana* and *Casuarina rumphiana* may fill equivalent ecological roles and share membership of the same ecological guild. *Hydriastele costata* and *P. rumphiana* seem to share similar population establishment strategies, and both species naturally regenerate from seeds but not from suckers and both species produce relatively abundant seeds.

The abundance of *H. costata* seemed to increase with the cation exchange capacity. Soil cation exchange potential is linked with soil drainage capacity and well-drained soils contain high sand fractions (White 1997). The mean density of *H. costata* on hill slopes adjacent to coastal area was 72.4 individuals ha^{-1}, while on hill slopes far away from coastal area (inland) it was only 8.6 individual ha^{-1}. The absence of *H. costata* from converted forest is an indication that this species is intolerant of habitat disturbance, in which growth is prevented. In addition to the apparent preference for dry, well-drained soils, *H. costata* appeared to be more common in sites with higher electrical conductivity and higher concentrations of major nutrients, especially Mg^{++} and Ca^{++}. Surprisingly, K^+ and Na^+ contents did not correlate significantly with the palm density and frequency. This may be due to the very low contents of these minerals at various sites studied.

Hydriastele costata often forms a prominent component of the coastal Waigeo vegetation. However, a high level of disturbance, such as forest clearance behind the Waifoi forest, has caused some colonies to decline. In heavily shaded inland sites of the reserve, the palm very scarcely occurs with only very few individuals found. The palm is not a true gap exploiter and appears to be unable to take advantage of unstable canopy conditions (i.e., slightly disturbed habitats) and to become established in ecologically limited spaces.

Slope angle and vegetative cover affect moisture effectiveness by governing the ratio of surface run-off to infiltration. As drainage deteriorates, the oxidised soil profile of well-drained sites is transformed into the mottled and gleyed profile of a wet soil. The influence of slope on soil texture and water holding capacity partly determines the levels of available mineral nutrients, and thus the establishment and spatial distribution of vegetation. Soils on slopes tend to be coarser and better drained than those on flat ground where run-off creates accumulations of small soil particles (House 1984, White 1997, Hall 2004).

It seems that generative propagation through seed germination is most important for colony maintenance, while seed dispersal must be important for the establishment of new colonies far removed from reproductive adults through water transport (hydrochory). Seeds were sometimes seen to germinate in canopy gaps. Curiously, seedlings were often absent beneath the crowns of mature individuals. As light exposure is important for flowering and successful fruit set, and because the crowns of this palm occupy mainly the upper canopy, it is not surprising that fertile adult plants were relatively abundant. No effective dispersers of *H. costata* seeds were encountered during this study. Due to small seed size, long-distance travellers such as frugivores and granivores (pigeons) are likely to be potential dispersal agents.

Conclusion

Relationship between Mg^{2+} and Ca^{2+} content and the occurrence and abundance of *H. costata* was detected. Four species *(Casuarina rumphiana, Decaspermum bracteatum, Baeckea frutescens,* and *Pinanga rumphiana*) were strongly associated with *H. costata*, indicating the same habitat requirements and ecological preferences. However, it is still unclear whether rapid drainage or intolerance to low nutrient content determines the occurrence and abundance of *H. costata* and what factors drive the interspecific association. If intolerance to low nutrients is the case, the absence of the palm from sites with high nutrient contents may be due to rapid water shortage, particularly on steep slopes and hill tops. Otherwise, it may be due to its slow intrinsic growth rates during the seedling stages, excluding it from sites where plants with faster growth rates predominate. All of these are possible explanations of the research findings and thus further research is recommended. The information gleaned from this study will be useful to reserve managers to quantify the palm's occurrence and abundance in the reserve, guide an effective monitoring program, and possible use of the palm as an indicator of habitat conditions.

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Hybrid zone characteristics of the intergeneric hybrid bamboo × *Gigantocalamus malpenensis* (Poaceae: Bambusoideae) in Peninsular Malaysia

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ABSTRACT. The natural intergeneric hybrid bamboo × *Gigantocalamus malpenensis* and its parental species, *Dendrocalamus pendulus* and *Gigantochloa scortechinii*, were mapped along a 4-km stretch of the Gombak valley in Peninsular Malaysia. Hybrid clumps were associated only with *D. pendulus*, which implied the latter was the seed parent, and not with *G. scortechinii*, which occupied only broader, gentler sites available for its establishment at the southwest and mid-southern parts of a southwest-to-northeast trending corridor of disturbance associated with expressway construction some three decades before. The effects of landscape-level disturbance on vegetation and plant demographic changes, gene flow and breeding dynamics are discussed.

Keywords. Bamboo, *Dendrocalamus*, disturbance, × *Gigantocalamus*, *Gigantochloa*, hybrid zone, hybridisation, Peninsular Malaysia

Introduction

A bamboo morphologically intermediate between *Gigantochloa scortechinii* Gamble and *Dendrocalamus pendulus* Ridl., two common bamboo species in the foothills of the Peninsular Malaysian Main Range, was discovered in two different localities (Perak and Selangor states) in Peninsular Malaysia (Goh et al. 2011). The hybrid nature of the morphologically intermediate taxon was demonstrated using partial Granule-Bound Starch Synthase (*GBSS*) I sequences, and this natural intergeneric hybrid was named × *Gigantocalamus malpenensis* K.M.Wong (Goh et al. 2011). Of its two known localities, the second, in the Gombak valley in Hulu Gombak, Selangor, Peninsular Malaysia, included a substantial number of clumps along a significant span of the valley, and it was decided to attempt to understand the population characteristics better, especially when its parental populations were also well represented in the same valley.

The reproductive behaviour of this hybrid, especially in comparison to its wild parental species, was of special interest. While entirely vegetative stands of both *Gigantochloa scortechinii* and *D. pendulus* are frequently encountered (Wong 1995a, b), they are known to flower gregariously, i.e., synchronised flowering of a significant number of clumps within a localised population (Burgess 1975; Wong 1995a, b), although 'diffuse-sporadic flowering' (isolated whole-clump flowering at irregular intervals in natural populations) is also known (Wong 1995a, b). Caryopses (the one-seeded fruits of bamboos) and seedlings are easily encountered in the wild amid gregarious flowerings of these two species. However, a certain degree of self-incompatibility would be expected because caryopses and seedlings have not been found with isolated flowering clumps of *G. scortechinii*; and only a very low level of caryopsis formation was found with the flowering of an isolated clump of *G. rostrata* K.M.Wong, a related species (Wong 1995b). Goh et al. (2011) reported that a solitary cultivated clump of the hybrid from Perak had flowered quite soon after it grew into mature size and died completely afterwards, with no caryopses formed. Flowering and fruiting of the hybrid in the wild has not been recorded until the discovery of the Selangor population at Hulu Gombak.

Study site, methods and materials

The study site was in the Hulu Gombak area (101°44'30" to 101°46'E, 3°19'15" to 3°20'25"N) of Peninsular Malaysia's Selangor state. The valley was steep-sided but the terrain beside the Gombak River was around 250–400 m elevation in this area. The portion of the Gombak valley investigated resembled a southwest-to-northeast corridor, flanked by the Karak Expressway to the north of the Gombak River, and by the smaller, old Gombak Road to the south. The construction of the Karak Expressway just before 1980 was impactful, involving many slope cuts, infills and bridging across generally steep inclines. Wayside spaces abutting the Expressway and between that and the Gombak River are frequently occupied by successional stands of low vegetation, and there are patches of *Acacia mangium* Willd. cultivated for forestry or site-greening purposes but occasionally escaping.

We used a GARMIN GPSMAP 60CSx handheld GPS unit to obtain satellite readings of location coordinates for clump positions of the hybrid × *Gigantocalamus malpenensis* and its parental species, *Gigantochloa scortechinii* and *D. pendulus*, along a 4-km stretch of the Gombak valley, where these bamboos occurred in September, 2009. Clumps were noted as 'vegetative' (complete lack of flowering activity), 'flowered' (with signs of past/recent flowering but no fresh flowers seen), or 'flowering' (with fresh flowering persisting). An estimate of relative clump maturity was obtained by classifying clumps as 'mature', when there were culms exceeding 3.5 cm diameter at 1.5 m height present, or 'young', when there were no culms exceeding 3.5 cm diameter. This is based on the observation that there would be larger culm internode diameters produced with increasingly older clump age until a maximum that was representative of the species, so that younger clumps typically produced culms of smaller diameter (Holttum 1958, Wong 2004).

The coordinates were transferred from the GPS unit to a personal computer using software provided by the manufacturer. The data was then viewed in a Google Earth 5.2 scene of the Hulu Gombak area (on 1 Oct 2009) with the location coordinates obtained represented by symbols plotted onto the satellite view. A tracing of this was made (Fig. 1) to show the main Gombak River flanked by the Karak Expressway and the Gombak Road, as well as required contours to represent the physical landform, together with plotted points showing the locations of bamboo clumps recorded.

Results

The results of the population census for the three bamboo taxa are summarised in Table 1, with locations of × *Gigantocalamus malpenensis* and its parental species, *Gigantochloa scortechinii* and *D. pendulus*, mapped in Fig. 1.

Distribution of taxa across the hybrid zone

The respective sites of the parental species were interesting: *G. scortechinii* occupied flatter or gentler, streamside places along the Gombak River, adequately represented at the southwestern and mid-southern parts of the valley, whereas *D. pendulus* typically occurred on steeper hillsides along the same valley. Hybrid individuals occurred together with *D. pendulus* clumps towards the northeastern part of the valley, and not with the *G. scortechinii* population.

Bamboo flowering and seeding during the census

There were 55 individual clumps of *D. pendulus* (incl. 1 young clump as defined for this study) and 67 clumps of *G. scortechinii* (no young clumps) recorded in the study area. All were vegetative, showing no sign of flowering.

Among 48 clumps of the hybrid, 35 (c. 73%) were vegetative at the time of the census and 13 were recently in flower or were still flowering (Table 1). These

Table 1. Observed clumps of the hybrid × *Gigantocalamus malpenensis* and its parental species *Dendrocalamus pendulus* and *Gigantochloa scortechinii* along the Hulu Gombak valley, Peninsular Malaysia: summary of some biological attributes (vegetative vs. reproductive states; relative maturity). Clumps were noted as Vegetative, Flowered (signs of recent flowering but no fresh flowers seen), or Flowering (with fresh flowering persisting). Clump relative maturity: Mature (indicated by presence of culms exceeding 3.5 cm diameter at 1.5 m height) or Young (no culms exceeding 3.5 cm diameter present).

Taxon	Number of recorded clumps	Clumps in vegetative state	Live clumps that had flowered / were flowering during census	Dead clumps that had flowered
Dendrocalamus pendulus	55	55 (incl. 1 young clump)	0	0
Gigantochloa scortechinii	67	67 (incl. 0 young clumps)	0	0
Hybrid (× *Gigantocalamus malpenensis*)	48	35 (incl. 7 young clumps)	7 had flowered + 3 still flowering	3

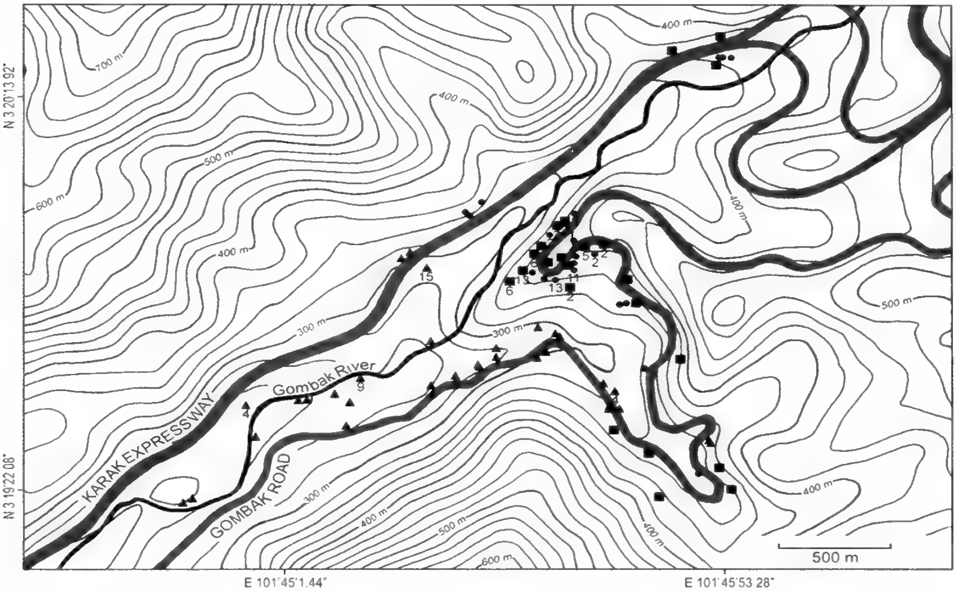

Fig. 1. The Gombak River, Gombak Road and Karak Expressway (thick lines), and locations of the hybrid × *Gigantocalamus malpenensis* (dots) and its parental species, *Dendrocalamus pendulus* (squares) and *Gigantochloa scortechinii* (triangles), in Hulu Gombak, Selangor, Peninsular Malaysia.

vegetative clumps included only seven young clumps (i.e., clumps without any culms exceeding 3.5 cm diameter). It is reasonable to assume that this represented an establishing hybrid population originating from possibly just 1–2 parental seeding events, which must be rare, but when the flowering of both parental species on site must have coincided. Flowering in the hybrid population appears to have involved only a small proportion of hybrid individuals.

It stands to reason that the population of hybrid clumps found probably represented F1 hybrid material. Seeding of the F1 must have been absent or very limited, and seedling survival negligible, because caryopses were not found among the flowering material, and young seedlings were absent on site among the flowering hybrid clumps, in spite of a good number of these (10 out of 13) having completed flowering and not having any more fresh flowering branches on them during the census. Thus, the presence of an F2 generation was not detected although a cohort of flowering F1 hybrids was present.

Discussion

Hybrid zone characteristics

The near segregation of the parental populations was compatible with what is known about their ecological distribution: *D. pendulus* is more typical of steeper hillsides, whereas *G. scortechinii* prefers gentler slopes and frequently spreads onto the disturbed and logged-over plains (Wong 1995b). The availability of sites suitable for *G. scortechinii* thus appeared to constrain establishment of that species to the southwestern and mid-southern parts of the study area. In particular, a protruding ridge in the middle of the study area had an abundance of *D. pendulus* established on its steep sides (Fig. 1).

The distribution of the hybrid relative to the two parental species (the hybrid being associated with *D. pendulus*) suggested that *D. pendulus* was the maternal parent for the hybrid cohort investigated. Caryopses are expected to have poorer dispersal ability compared to pollen, and bamboo pseudospikelets and caryopses mostly fall around the parent clump (Ridley 1930; Wong 1995a, b). A previous attempt at deducing the direction of the cross between the parental species, using cpDNA that was likely to have been maternally inherited and including a broader geographical sampling of the species, was equivocal probably because of complex patterns of inheritance for which past reciprocal crosses between taxa followed by introgression (sensu Anderson 1948) could not be ruled out (Goh et al. 2011).

Ecological implications

Why were these hybrids not detected earlier, although this part of the Gombak valley has been a routinely well-botanised locality? The hybrid bamboo was not observed at all during the several visits annually to the study area from 1980, when the Karak Expressway construction was being completed, to 1988, and 1996–2007 (K.M. Wong, pers. obs.). Hybrid population characteristics, particularly its distribution, suggest comparatively recent establishment. We suggest that the "corridor of change" brought about by development (i.e., opening up) of the Karak Expressway (parallel to this part of the Gombak valley) just before 1980 was a key factor that may have predisposed the hybridisation event. This enormous cleared corridor caused greater openness, spread and an increased abundance of both *D. pendulus* and *G. scortechinii* (and other pioneer or early successional plant species), as well as the removal of forest tree cover that probably served as a natural impediment to genetic exchange between the bamboo species. In the dense vegetation of tropical rain forest, high humidity could dampen pollen, increasing their difficulty in remaining airborne, and rain often removes airborne pollen; also the dense tree canopy tends to be an effective filter of airborne pollen (Turner 2001).

Greater exposure along this corridor had probably increased chances for air currents carrying pollen from *G. scortechinii* clumps in flatter terrain at one end (southwest) to find hillside patches occupied by *D. pendulus* near the other end (northeast). The tendency for both *D. pendulus* and *G. scortechinii* to flower gregariously or diffuse-sporadically from time to time probably increased the possibility of coincident flowering and cross-fertilisation.

Will the hybrid persist? At the time of the census, it could be said that the hybrid was beginning to establish. It was represented by 48 clumps, but over 70% remained vegetative while 13 clumps had come into flower. This suggests there could be some variability with respect to age at onset of flowering. The distribution of hybrid offspring clumps among so many maternal clumps (individuals) in this case also implies a range of resulting heterozygosity in the hybrid offspring that would bring increased variability even in flowering time (or its associated vegetative longevity). There were also several clumps that had flowered but which were producing new culm shoots. The survival of such new culm shoots was not certain, but again represented a potential for regeneration following flowering, which has been noted for clumping bamboos that exhibit whole-clump flowering (Wong 1995a, b). Thus, there appears to be a good prospect for the survival of the hybrid.

Hybrids are probably more common among related species (e.g., Okada 1990, Kiew et al. 2003, Gravendeel et al. 2004) than between genera, but intergeneric crosses are also known for other plant groups (e.g., McKenzie et al. 2008). Plant taxa have also been surmised to have originated from intergeneric hybridisation events (Tara 1977, Wallace & Jansen 1995) and hybridisation between genetically divergent lines have been known to give more vigorous progeny (Edmands 2002). The potential for viable backcrosses and advanced-generation hybrids cannot be presently estimated.

Conclusion

Continuing research also examines generic boundaries among the group of bamboos classified as the Bambusinae subtribe, which includes *Dendrocalamus* and *Gigantochloa*. This includes the difficulties of classifying a mystifying complex of bamboos that have defied simple lineage studies so far (e.g., Yang et al. 2008, Stapleton et al. 2009, Yang et al. 2010, Goh et al. 2010), so that the use of more gene regions, including from both nuclear and plastid domains, would be important. The present case study of hybridisation between *D. pendulus* and *G. scortechinii* (Goh et al. 2011, this study) confirms that natural hybrids do form in the tropical Southeast Asian landscape, especially when ecological barriers between taxa change in nature. Elsewhere, Clark et al. (1989) and Triplett et al. (2010) have documented interspecific hybridisation among American bamboos. We have suggested (Wong 2004, Goh et al. 2010, Goh et al. 2011; Wong et al., in prep.) that the role of hybridisation in the evolution of Tropical Asian bamboos could have been underestimated, mostly because such hybrids are difficult to detect and confirm. Hybridisation is a significant feature of gene flow and evolutionary processes (Rieseberg 1995, Arnold et al. 2001) and extensive adaptive radiation can occur after hybridisation (Givnish 2010). It should be expected that among highly complex taxonomic groups such as the woody bamboos, hybridisation and introgression studies would hold the key to a better understanding.

In conservation terms, we have hardly any documentation of the effects of environmental change (especially through vegetation removal or degradation) on the reproductive behaviour and gene flow among plants in Southeast Asia. The primary concern is perhaps correctly placed on the decimation or reduction of plant populations in an affected area (Laurance et al. 1997), giving emphasis on potentially adverse effects associated with breakdown of long-established and naturally viable pollinator, breeding, dispersal and establishment biology (e.g., Washitani 2000). This study has demonstrated how landscape-level changes equivalent to that seen with development in the Hulu Gombak area may predispose the plant life to changes in reproductive and ecological behaviour. In this case, the chance of hybridisation occurring between *D. pendulus* and *G. scortechinii*, the two abundant species of bamboo in the Hulu Gombak valley, was probably increased in the aftermath of landform and vegetation changes, facilitated by removal of natural physical barriers that have helped maintain reproductive isolation of the species, and the products of hybridisation began establishing only nearly 30 years following disturbance. Changes in the environment would be expected to alter relative species abundances, plant establishment, and processes or patterns (including direction and symmetry) of gene flow and breeding. Hybridisation would bring along fitness consequences influenced by the extent and quality of the breeding interaction.

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The ecology of ultramafic areas in Sabah: threats and conservation needs

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ABSTRACT. Ultramafics are characterised by high concentrations of magnesium and nickel, low concentrations of calcium, low water retention capacity and low concentrations of essential plant nutrients in soils derived from this substrate. These extreme chemical soil condition force plants to adapt to survive. Sabah is one of the richest areas in the world for plant diversity on ultramafic substrates. A range of species, including a number of pitcher plants (Nepenthaceae), orchids (Orchidaceae) and trees and shrubs are endemic to ultramafic areas in Sabah, often occurring on a few, or even just a single, site. Ultramafic vegetation types in Sabah are severely threatened by land-clearing activities. Although only a small minority of the geological substrates in Sabah are ultramafic, ecosystems on these substrates have a disproportionately high number of endemic and rare plant species. Destruction of these types of ecosystems, in particular, can potentially result in extinction of plant species.

Keywords. Endemism, Mount Kinabalu, rare species, Sabah, serpentine, ultramafics

Introduction

Preliminary research suggests that the Malaysian state of Sabah may be one of the richest areas in the world for plant diversity on ultramafic substrates. Kinabalu Park, covering approximately 1200 square kilometres, has in excess of 900 plant species occurring on ultramafics. This extremely high diversity is a consequence of the immense biodiversity of the Malesian region itself, as well as the locally diverse edaphic and climatic conditions. Generally in the Malesian region, ultramafic vegetation types have lower stature and different species composition compared to lowland dipterocarp-forest (Proctor & Nagy 1992). The edaphic stresses that ultramafic substrates exert on plant survival have resulted in high numbers of endemic species on these substrates.

Ultramafic rocks and substrates

Ultramafic (or 'ultrabasic') substrates are found all around the world. The often-used geological term 'serpentine' refers to lizardite, antigorite and chrysotile, but ecologists use it to describe the ecology of soils derived from ultramafic substrates (Coleman & Jole 1992). Ultramafics are found in tectonic chunks ('ophiolite suites').

which are fragments of the upper mantle obducted in continental margins on ocean floors (Coleman & Jole 1992). In Sabah, ultramafics (predominantly in the form of the mineral peridotite) that have been raised above sea level weather to iron- and nickel-rich laterites (Baillie et al. 2000). Such soils are characterised by very high concentrations of magnesium and nickel, both of which may be phytotoxic, have low water retention capacity, low available phosphorus concentrations (partly due to phosphorus-immobilising ferric sesquioxides) and low concentrations of other essential plant nutrients such as nitrogen and potassium (Baillie et al. 2000).

The ultramafic effect ('serpentine syndrome')

The evolutionarily challenging selection forces that ultramafics exert on plants is a result of the extraordinary geochemistry (Rajakaruna & Baker 2006). The excess of magnesium, and specifically the very low calcium to magnesium ratio (<1) in soils derived from ultramafic substrates, is an important factor in determining species composition and structure of vegetation on ultramafic substrates (Brooks 1987). The foliar concentration of magnesium is often significantly higher in plants growing on ultramafics, while calcium concentrations are often significantly lower (Brady et al. 2005). Extremely high nickel concentrations in such soils can also be limiting to the growth of many plant species. The bioavailable and thus potentially phytotoxic concentration of nickel in the soil depends on soil clay content, organic exudates in the rooting zone, soil moisture pH and the presence of other divalent ions such as calcium and magnesium.

Another important factor defining the structure and species composition of ultramafics is water stress. Many plants found on ultramafics have morphological adaptations to minimise water requirements and water loss in order to survive in drought conditions (Brady et al. 2005). Such adaptations include a generally low stature, small-crowned growth-form and other characteristics such as glaucous leaves and sclerophyllous and microphyllous morphologies. Examples of vegetation types in which many plants clearly display such adaptations are the graminoid vegetation on higher elevations on Mt. Tambuyukon and the stunted vegetation at Mt. Silam (Bruijnzeel et al. 1993). Morphological adaptations that evolved to reduce transpiration are also likely to minimise nickel and magnesium uptake. The low water retention capacity of most ultramafic soils might induce water stress, but may also increase the toxicity of magnesium and nickel by the concentration effect in the soil solution (Proctor & Nagy 1992). In addition, water stress and drought can increase the susceptibility of vegetation to fire. Prolonged dry periods that may occur due to the El Nino effect often result in fires affecting the ultramafic vegetation communities of Mt. Kinabalu. Aiba & Kitayama (2002) showed that the growth rates of trees on ultramafics are lower than those at equivalent altitudes on non-ultramafics, but they have also shown that the mortality rate during droughts is distinctly lower on ultramafics. The recurrence of fires delays succession and therefore prevents development of tall vegetation types. Furthermore, the burning of leaf litter during fire could also have an effect on the soil nutrient status by increasing the availability of phosphorus and mineralising organic matter.

The environmental and edaphic factors mentioned in the proceeding paragraph have, taken together, been termed the 'serpentine syndrome' (Jenny 1980), a 'syndrome' expressed through the combined characteristic morphology, physiology and ecology of these plant communities that likely results from a dynamic interplay of the above-mentioned factors (Brady et al. 2005). Besides the geochemical anomalies, other prevailing environmental and edaphic conditions may also be important in determining the specific vegetation composition and structure of such plant communities. Soil depth and the degree of exposure to wind, for example, may also be contributing factors that restrict the successful survival of plants on ultramafics.

Hyperaccumulators of nickel in Sabah

Some plants have the remarkable physiological capacity to accumulate shoot nickel at levels 100-10,000-fold greater than levels in non-accumulators (Lasat 2001). Such 'hyperaccumulators' are confined to ultramafics because that substrate is the largest and most widespread metal-enriched habitat on a global scale. It is an exceptionally rare phenomenon with only 1–2% of plant species found on ultramafics being classed as hyperaccumulators. As of 2010, some 400 nickel hyperaccumulator species have been described (Baker 1981, Baker & Smith 2000). Nickel hyperaccumulators are found in many different genera across at least 45 plant families (Baker et al. 1999). As such, nickel hyperaccumulators have a great variety of growth forms, ecophysiological characteristics and ecological requirements (Pollard et al. 2002). The plant families that are most represented are Euphorbiaceae, Brassicacea, Asteraceae, Flacourtiaceae (Salicaceae), Buxaceae and Rubiaceae (Reeves 2003), illustrating that this phenomenon has independently developed multiple times on ultramafics. Nickel hyperaccumulators are relatively easy to identify by chemical analysis of dried foliage in the laboratory or in the field by pressing fresh leaves against white test paper impregnated with dimethylglyoxime ('DMG'), which is a nickel-specific colorimetric dye (Baker et al., 1992a).

A number of hyperaccumulators have been found in Sabah, including: *Rinorea bengalensis* (Wall.) Kuntze, *Phyllanthus balgooyi* Petra Hoffm. & A.J.M.Baker, *Dichapetalum gelonioides* (Roxb.) Engl. ssp. *tuberculatum* Leenh. and *Shorea tenuiramulosa* P.S.Ashton. The small tree or scrambler, *Dichapetalum gelonioides ssp. tuberculatum*, has up to 25 mg/g nickel in its dried foliage (Reeves 2003). While hyperaccumulators are typically recognised on the basis of the concentrations of metals in the foliage, other plant parts may have very different metal concentrations. For instance, Reeves (2003) cites values for phloem tissues of the shrub *Phyllanthus balgooyi* of up to 90 mg/g nickel on a dry weight basis. This is a widespread shrub on ultramafics in Sabah (as well as in the Philippines) and it has only recently been described formally (Hoffmann et al. 2003). Prior to this, it was provisionally recognized as *Phyllanthus 'palawanesis'* (Baker et al. 1992b).

Epiphytes on ultramafics

Epiphytes are an ecologically important part of the plant diversity on ultramafics in Sabah, particularly at higher altitudes. Epiphytes may be sensitive to the chemical composition in the host tissues and may absorb elements, such as nickel, from their host. However, the precise ecological relationship between epiphytes and their host is very poorly understood. In New Caledonia, Boyd et al. (2009) found that epiphytes (mosses and liverworts) growing on nickel hyperaccumulator hosts contained higher levels of nickel than those growing on non-hyperaccumulator hosts. Even more so, the epiphyte nickel concentrations often exceeded the threshold of nickel hyperaccumulation (Boyd et al. 2009). This indicates that the capacity of epiphytes to grow on hyperaccumulators depends on their capability to tolerate high nickel concentrations, which may in turn define the spatial and ecological attributes of epiphyte community composition (Boyd et al. 2009). There is limited evidence from Mt. Kinabalu were several epiphytic orchids are known only from ultramafic substrates, suggesting important correlations between the chemical composition of substrate and host. In addition to potential chemical relationships, the open and low-statured structure (with, as a result, higher sunlight intensity, higher surface temperatures, lower humidity and higher wind exposure) of many ultramafic vegetation types is undoubtedly important for the distribution and relative abundance of epiphytes on ultramafics.

Endemism on ultramafic substrates

Whittaker (1954) categorised three general characteristics common among vegetation types on ultramafics: (a) low stature and biomass production; (b) high levels of endemism; and (c) distinct differences from vegetation in surrounding areas. Based on these characteristics, Whittaker (1954) attributed the 'serpentine syndrome' to three causes: the edaphic or geochemical; the plant species-level (autecology); and the plant community-level (synecology). The preponderance of endemism of species occurring on ultramafic substrates in Sabah differs strongly between areas. High levels of endemism are generally associated with especially isolated areas, either geographic or altitudinal. Some species may have a high affinity for ultramafic substrates, being more abundant or even solely confined to such areas, while others have wide ecological amplitudes and occur on different substrates. Species endemic to ultramafics may be paleo-endemics; species for which their population have become confined to ultramafics due to competition elsewhere (Baker & Whiting 2002), or neo-endemics which have evolved *in-situ* from closely-related species.

Ultramafics in Sabah

The geology of Sabah, Malaysia, is mainly composed of sedimentary rock, such as sandstone and shale, but about 3500 square kilometres (4.6% of total landmass) of

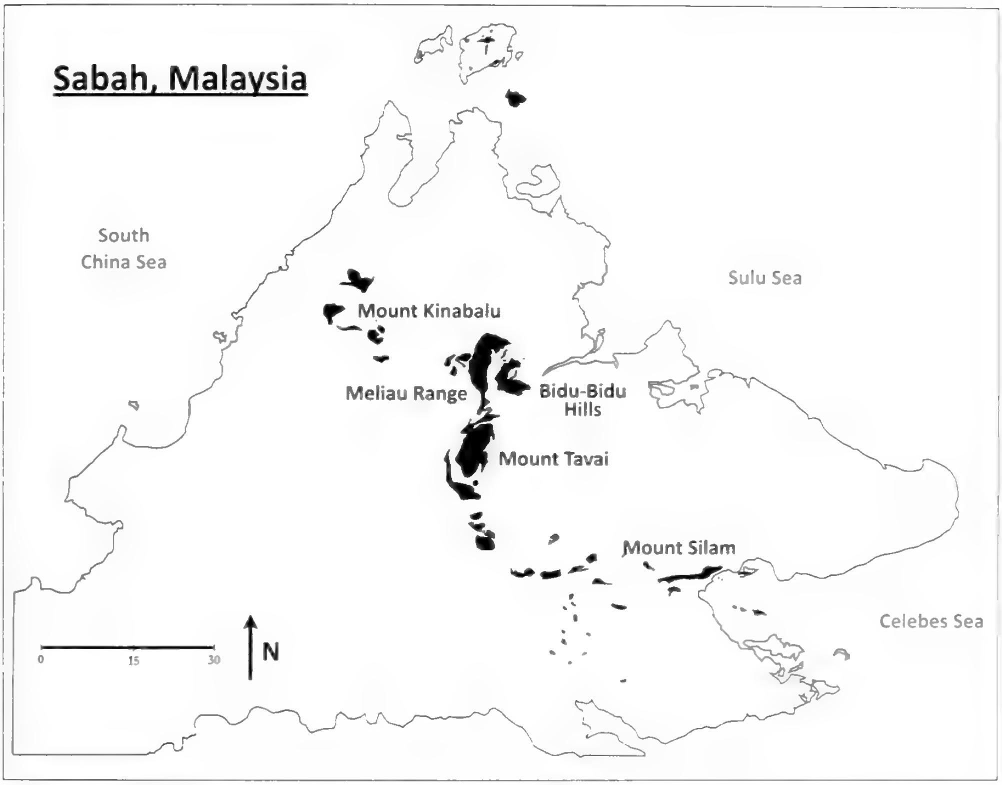

Fig. 1. Delimitation of ultramafic outcrops based on the map 'Igneous Rocks of Sabah, Malaysia' by Geological Survey, Borneo Region, Malaysia, 1965. In the map, the most extensive ultramafic outcrops are featured, including Mount Kinabalu, Mount Silam, Mount Tavai, Meliau Range and Bidu-Bidu Hills.

ultramafics occur (Proctor et al. 1988, Repin 1998). The most extensive ultramafic outcrops are found in the Meliau Range, at Mt. Tawai, the Bidu-bidu Hills, Mt. Silam and around Mt. Kinabalu (Collenette 1964) (Fig. 1). Ultramafics are found from sea level (on islands in the Darvel Bay area) up to nearly 2900 metres above sea level (on Mt. Kinabalu). Studies of the plant diversity on ultramafics are extremely limited in Sabah. The Sabah Forestry Department (2005) has undertaken some general site reconnaissance at Mt. Tawai and the Bidu-Bidu Hills and described three main types of ultramafic vegetation: (1) lowland ultramafic forest, in which dipterocarps dominate; (2) hill forest in which *Casuarinaceae* dominate but also some dipterocarps are found; and (3) hill and lower montane mixed dipterocarp forest. Mt. Silam near the town of Lahad Datu has extensive ultramafic vegetation and has been the subject of more extensive research (Proctor et al. 1988, Proctor et al. 1989, Bruijnzeel et al. 1993). Although this mountain is only 884 m high, it ranges from lowland dipterocarp-dominated forest to stunted *Myrtaceae*-dominated vegetation (Proctor & Nagy 1992). Ultramafics on the islands in Darvel Bay are often composed of mono-specific stands of *Casuarina nobilis* Whitmore (Fox & Hing 1971). The plant diversity of Mt. Kinabalu has been the subject of extensive research (see Beaman & Beaman 1990; Beaman et al. 2003), but the ecology of ultramafics has so far only been studied specifically by Repin (1998).

Ultramafics around Mt. Kinabalu

Barthlott et al. (2007) lists the northern part of Sabah as one of the top five global plant diversity centres, with more than 5,000 species per 10,000 square kilometres. Extensive research at Mt. Kinabalu, has revealed that the plant diversity is as high as 5000–6000 species (excluding mosses and liverworts but including ferns), comprising over 200 families and 1000 genera (Beaman et al. 2003). Given that this plant diversity occurs in an area approximately only 1200 square kilometres, Mt. Kinabalu probably represents the most floristically biodiverse place in the world (Beaman et al. 2003). The high biodiversity at Mt. Kinabalu is mainly the result of the different climatic zones, due to altitudinal differences, the large array of soils including ultramafics ('geodiversity'), the distinctiveness of habitats and the proximity of older mountain ranges (Mt. Kinabalu is geologically very young), which provide a 'species dispersion base' (Beaman et al. 2003). At elevations of 1700 m and above, ultramafic vegetation is characterised by the dominance of (1) *Tristaniopsis elliptica* Stapf, (2) *Leptospermum javanica* Sm.– *Tristaniopsis elliptica* Stapf, and (3) *Leptospermum recurvum* Hook.f. - *Dacrydium gibbsiae* Stapf (Kitayama 1991). On lower elevations, *Gymnostoma sumatranum* (Jungh. ex de Vriese) L.A.S.Johnson and *Centhostoma terminale* L.A.S.Johnson are distinctive (Beaman & Beaman 1990). High on Mt. Kinabalu (around 2900m) the vegetation on ultramafics is rather bare and consists only of herbs such as *Schoenus curvulus* F. Muell., *Euphrasia borneensis* Stapf and *Machaerina falcata* (Nees) Koyama. The graminoid vegetation types on the summit of Mt. Tambuyukon and at the spur of Marai Parai are another characteristic of local ultramafic vegetation types, with endemic species such as the pitcher plant *Nepenthes rajah* Hook.f. and the herb *Scaevola verticillata* Leenh..

Mt. Kinabalu's ultramafic vegetation is typified by endemics from the Nepenthaceae family, which are confined to ultramafics such as the earlier mentioned *Nepenthes rajah* Hook.f. , as well as *N. burbidgeae* Hook.f. ex Burb. and *Nepenthes macrovulgaris* J.R.Turnbull & A.T.Middleton and a number of endemic orchids such as *Paphiopedilum rothschildianum* (Rchb.f.) Stein, *Paphiopedilum hookerae* (Rchb.f.) Stein *var. volonteanum* (Sander ex Rolfe) Kerch., *Paphiopedilum dayanum* (Lindl.) Stein, *Corybas kinabaluensis* Carr, *Arachnis longisepala* (J. J. Wood) Shim & A. Lamb and *Platanthera kinabaluensis* Kraenzl. ex Rolfe in Gibbs.

In addition, a range of trees, shrubs and herbs are ultramafic endemics at Mt. Kinabalu, including: *Magnolia persuaveolens subsp. rigida* Noot., *Embelia cordata* Philipson, *Syzygium dasyphyllum* Merr. & L.M.Perry, *Syzygium exiguifolium* Merr. & L.M.Perry, *Syzygium myrtillus* (Stapf) Merr. & L.M.Perry, *Eriobotrya aff. bengalensis* (Roxb.) Hk.f., *Hedyotis protrusa* Stapf, *Lasianthus membranaceus var. firmus* Stapf, *Urophyllum subanurum* Stapf, *Wikstroemia indica* (L.f.) C.A.Meyer and *Elatostema bulbothrix* Stapf (Beaman & Anderson, 2004).

Only a few tree species are currently understood as true ultramafic endemics. These include *Borneodendron aenigmaticum* (Meijer 1964), *Dacrydium gibbsiae*

Stapf and *Pittosporum silamense* J.B.Sugau. Some other species, such as *Buchanania arborescens* (Blume) Blume, and dipterocarps such as *Dipterocarpus lowii* Hook.f., *Dipterocarpus ochraceus* Meijer, *Dipterocarpus geniculatus* Vesque, *Shorea tenuiramulosa* and *Shorea kunstleri* King are typical of ultramafics, but are not entirely confined to this substrate (Ashton 1982; Proctor, 2003)

Threats to ultramafic vegetation in Sabah

Ultramafic vegetation types in Sabah are severely threatened by land clearing activities, such as in the Meliau Range, Bidu-Bidu Hills, Mt. Silam and Mt. Tawai and a range of smaller sites. Despite the status of a protected forest reserve of these ultramafic localities, encroachment remains a problem, and many sites without legal protection have disappeared in recent years, such as Morou Porou and the Lohan Valley. Mt. Kinabalu and ultramafic sites within national park boundaries, such as Mt. Tamboyukon are safeguarded, but land clearing has made the national park a virtual 'island'. Although only a small minority of the geological substrates in Sabah are ultramafic, these areas have a disproportionately high number of endemic and/or rare plant species. Many plant species occur on only a few sites or even a single site and habitat destruction, if it occurred, could therefore potentially result in extinction.

Conservation and research priorities

Only very limited research on the ecology of ultramafics in Sabah has been undertaken to date. According to Baker & Brooks (1988), *"... the ultramafic regions of Asia are generally the least explored and poorly described of such regions in the world"*. Due to the lack of scientific information, it is difficult to formulate conservation strategies and priorities, although given the history of, and potential risk for further, habitat destruction, it is evident that many species endemic to ultramafics are threatened. The need for conservation and research has been made strongly by Repin (1998) who emphasised that scientific research and preservation of ultramafics in Sabah needs to be given utmost priority, particularly in those areas without legal protection, before there is any further destruction and loss.

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Cultivation and conservation of *Lilium philippinense* (Liliaceae), the Philippine endemic Benguet Lily

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ABSTRACT. *Lilium philippinense*, endemic to the Cordillera Administrative Region (CCR) of the Philippines, grows on steep mountain slopes of Benguet and the southwestern part of the Mountain province. The flowers, fragrant and used as wedding decorations, occur from late May to July. Recent observations indicate declining populations of this species, which is said to be difficult to grow. Under greenhouse conditions, seed and bulb germination show only 27.63% and 16.67% success, respectively. The apparently acute sensitivity of this species to environmental factors such as soil pH, light, humidity, air and soil temperature, and possibilities for *ex situ* cultivation, are discussed.

Keywords. Benguet lily, conservation, Cordillera Administrative Region, cultivation, endemic, *Lilium*, Philippines

Introduction

Lilium philippinense Baker (Liliaceae) is endemic to the Philippines (Elwes 1880) and occurs in the southern part of the Cordillera Central Range (CCR). Its fragrant, white, trumpet-shaped flowers sometimes have a reddish tinge at the corolla base, and annual mass flowering events are spectacular. The species grows among grasses such as *Themeda triandra*, *Miscanthus sinensis* and *Imperata cylindrica*. Each plant bears one or two flowers per stem, rarely three or four. The fruit is a capsule with numerous small seeds. At the end of the short flowering season, the floral parts wither and the capsule matures and eventually releases its seeds. Following the end of the growing season, only the subterranean bulbs remain.

This lily is known by local names such as *kanyon* or *luplupak* (Ilocano), *us-usdong* (Mt. Province Kankanai), *putputak* (Benguet Kankanai), *tuktukpao* (Kayan, Tadian), *swasoy* (Ibaloi), and *suyosoy* (Ikalahan). Each local name illustrates a unique characteristic of the plant. For instance, *suyosoy* means "flower of the mountain"; *us-usdong* means "to bow" referring to the pendulous flowers; and *kanyon* means "a bomb", illustrating the somewhat explosive expulsion of seeds when mature fruits dehisce. Descriptions of *L. philippinense* are provided by Chittenden (1956), Bailey (1960), Steiner (1960) and Madulid (2001). *Lilium philippinense* is morphologically similar to *L. formosanum* and *L. longiflorum*, which are endemic to Taiwan and Japan, respectively, and which grow well in the CCR. Often, horticulturists regard these three lilies as the same species and sometimes refer to them interchangeably. In the Benguet and Mountain provinces, this lily is often a favorite adornment for wedding ceremonies and special occasions because of its delicate white flowers and fragrance.

There is scanty research on *L. philippinense*. A monograph of the genus *Lilium* is the only published account that gives some basic information of this species (Elwes 1880). In the Philippines, of two undergraduate reports on *L. philippinense*, one describes shoot and root initiation of bulb scales using low temperature stratification and a rooting hormone. That study showed that root formation can be enhanced by treating bulbs at 3°C for 60 days; and more and longer roots are initiated by soaking the bulbs in Hormex, a rooting hormone, prior to planting (Alipio & Ladilad 2005). In vitro propagation of *L. philippinense* was demonstrated by Ampaguey et al. (2002), who showed that callus formation was enhanced with three different media used; unfortunately, field evaluation of calli was not tried. There have been no previous studies of seed germination in this species.

Recently, *L. philippinense* populations were reported to have declined due to human activities such as over-collection (Madulid 2001) and destruction of habitat including landuse conversion and road widening (Balangcod 2009). From a conservation perspective, it is important to understand the reproductive behaviour of a species. This includes seed and bulb germination in this case. As pointed out by Schemste et al. (1994), detailed information on the different stages in the reproductive cycle of a species may contribute basic information helpful to conservation management decisions. The aim of the present study was to determine the germination and survival capacity of seeds and bulbs of this species, taking into account factors such as relative humidity, light, air and soil temperature in the greenhouse, as well as elevation and geographic location of the original material. Specifically, this study was conducted to (1) evaluate the percentage germination of *L. philippinense* using seeds and bulbs; (2) determine which of the two propagules, the seed or bulb, has a better performance for *ex-situ* cultivation; and (3) compare the percentage germination of seeds and bulbs from different *L. philippinense* populations.

Materials and methods

Seeds and bulbs of *L. philippinense* were collected from 28 populations from the southern part of the CCR (Fig. 1). Elevation was determined using a Geographic Positioning System (GPS). The collection sites ranged from 873 to 2091 m elevation,

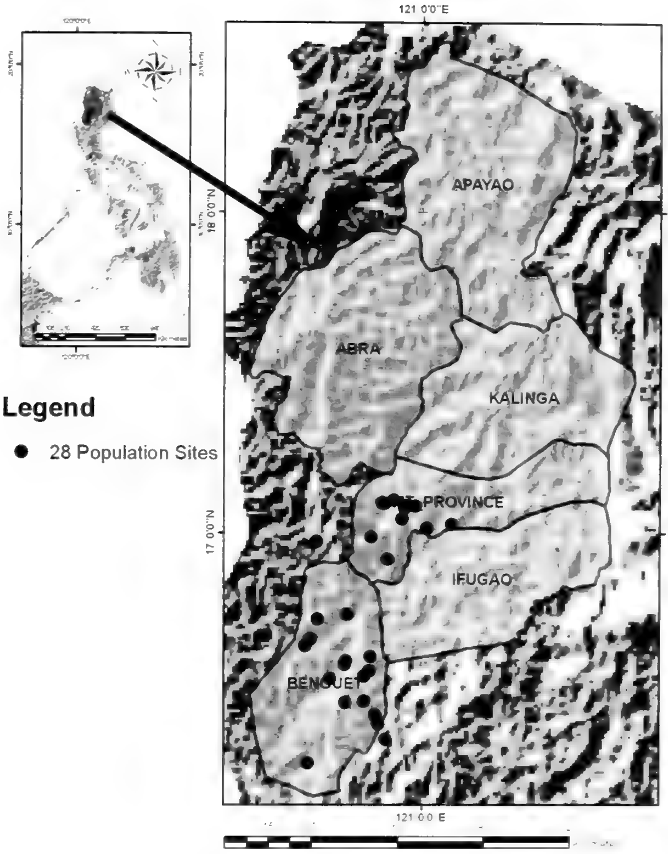

Fig. 1. Location of the 28 *Lilium philippinense* collection sites.

extending from 16°28'44" to 17°10'45"N and from 120°63'55" to 121°83'23"E. Collection of bulbs and seeds were made in August and September 2007 when mature seeds were available. Experiments were performed to investigate the germination capacity of seeds and bulbs and seedling survival of *L. philippinense* under greenhouse conditions that simulated the natural environment of this species. The environmental requirements of *L. philippinense* were noted in a separate study.

Seeds and bulbs were planted simultaneously after collection in standard plastic pots (11.43 × 10.16 cm) and maintained in a greenhouse. The germination capacity of the two propagules was evaluated 150 days from sowing. Observation was continued until the flowering phase to assess seedling survival over a 1-year period for bulb-originated plants, and over a 3-year period for seed-originated plants. Greenhouse parameters such as relative humidity, light, air and soil temperature were recorded and monitored. The daily average readings of different environmental factors were calculated and used for the monthly average within the first year.

The soil used in the experiment was collected from one of the population sites to conform to the soil requirements of *L. philippinense.* Soil parameters such as soil pH, organic matter content and phosphorus were analysed once before planting.

Descriptive, Correlation, and Principal Component analyses using Statistical Package for the Social Sciences (SPSS) were used to analyse the data. Graphs were generated using Microsoft Excel.

Results

The greenhouse condition

The air and soil temperature measured in the greenhouse for the duration of the experiment ranged from 22.57°C to 28.56°C and 19.07°C to 23.49°C, respectively. The relative humidity showed a minimum of 61.61% and a maximum 80.72% while light ranged from 581.53 footcandles (fc) to 1364.89 fc (Table 1). The Coefficients of Variation indicate that relative humidity, air and soil temperature did not vary significantly during the year, but that light varied slightly.

Relatively high air and soil temperatures were recorded from March to August and falls slightly in the succeeding months (Fig. 2). Light peaked in June with a mean value of 1363 fc. This corresponds with the time when *L. philippinense* starts to bloom in its natural habitat. Relative humidity oscillated uniformly throughout the year.

Of the four parameters measured in the greenhouse, correlation analysis shows that air temperature is highly and positively correlated with soil temperature (r = 0.867, p = 0.000) and negatively correlated with relative humidity with a correlation value of r = -0.657, p = 0.020 (Table 2). This suggests that there is positive relationship between air and soil temperatures. On the other hand, there is a negative relationship of air temperature and relative humidity.

The soil used in the experiment has a pH of 6.5, which is slightly acidic, a high organic matter content of 4.68 per gram of soil and available phosphorus of 9.04 ppm. The last is moderately low (PCARRD 1982). These quantities fall within the ranges of parameters recorded in a previous study (Balangcod 2009). The ecological parameters measured in the greenhouse were comparable with data obtained in the natural habitat (Balangcod 2009).

Table 1. Environmental factors measured in the greenhouse, October 2007 to November 2008.

	Relative Humidity (%)	Air temperature (°C)	Soil temperature (°C)	Light (foot-candles)
Minimum	61.61	22.57	19.07	581.53
Maximum	80.72	28.56	23.49	1364.89
Mean	70.50	25.71	21.25	921.54
Standard Deviation	6.92	2.43	1.42	232.18
Coefficient of Variation	9.82	9.45	6.58	25.19

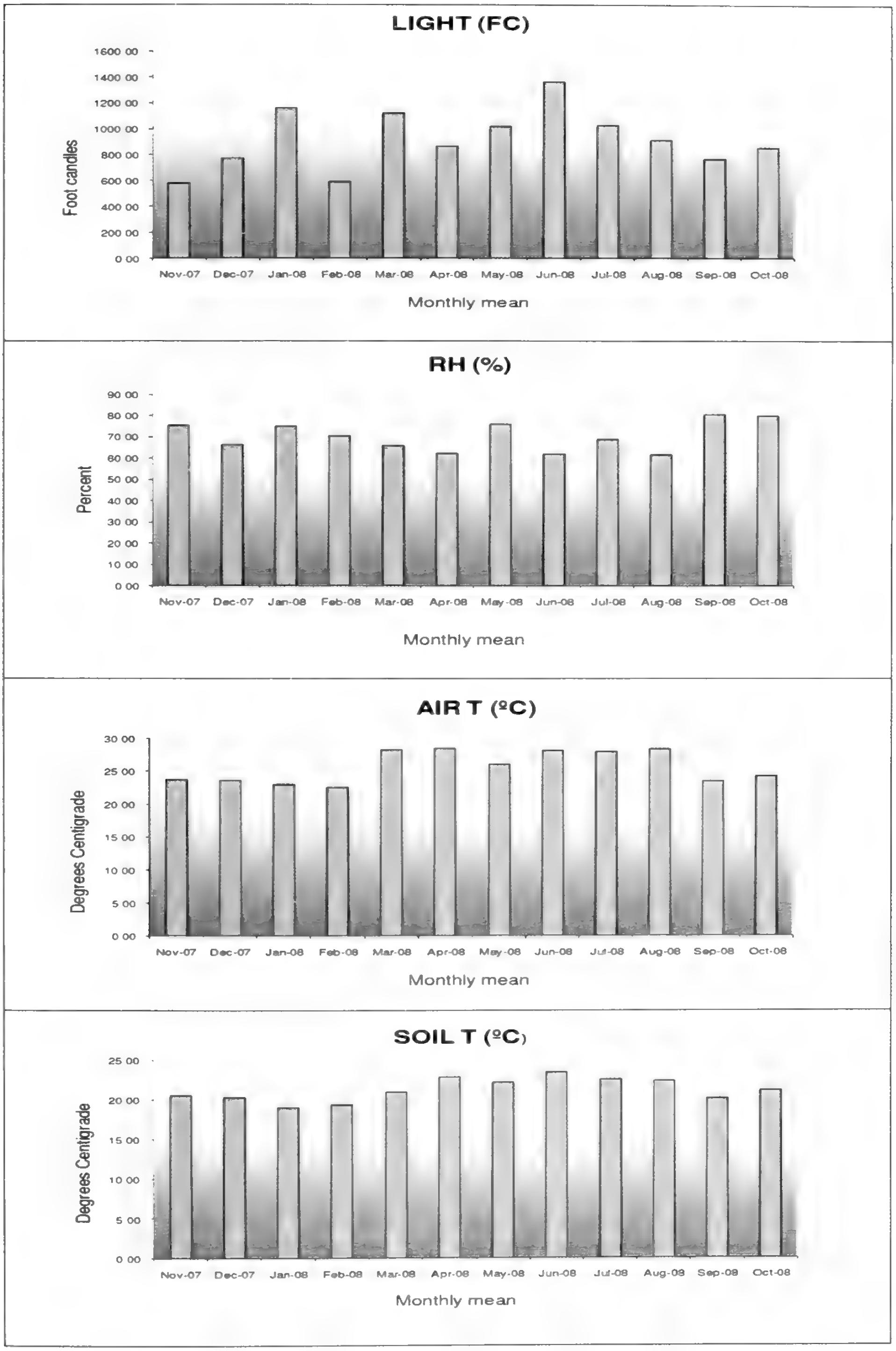

Fig. 2. Monthly means of environmental factors (from top: light, relative humidity, air temperature, soil temperature) measured in the greenhouse.

Table 2. Correlation analysis of environmental factors measured in the greenhouse. RH = Relative Humidity, temp = temperature.

			RH	Air temp	Soil temp	Light
Spearman's rho	RH	Correlation Coefficient	1.000			
		Sig. (2-tailed)	–			
		N	12			
	Air temp	Correlation Coefficient	-0.657*	1.000		
		Sig. (2-tailed)	0.020	–		
		N	12	12		
	Soil temp	Correlation Coefficient	-0.538	0.867**	1.000	
		Sig. (2-tailed)	0.071	0.000	–	
		N	12	12	12	
	Light	Correlation Coefficient	-0.434	0.434	0.420	1.000
		Sig. (2-tailed)	0.159	0.159	0.175	–
		N	12	12	12	12

Germination from bulbs

Of the total 252 bulbs collected from the 28 population sites, only 16.67% germinated. From the 16.67% that germinated, 57.14% seedlings developed till the flowering stage (Table 3).

The number of bulbs collected from each population differed because of availability. However, to solve the problem of sample size, the collection sites were pooled by performing hierarchical cluster analysis in SPSS (Fig. 3). Consequently, there were four clusters formed based on variables used, such as geographic location, elevation, number of bulbs and seeds, and percentage germination of both propagules. Characteristically, cluster 1 has an elevation range from 873 to 1103 m, cluster 2 has an elevation range of 1232 to 1354 m, cluster 3 has an elevation range between 1481 and 1794 m and cluster 4 has an elevation range from 1959 to 2091 m.

To determine if there were differences of variation in the number of bulbs collected and the germination capacity of the bulbs from different population sites within and among the clusters, one way ANOVA showed that all the values obtained were not significantly different, except for elevation (Table 4). This demonstrated that the population sites and the number of bulbs have no significant differences in their ability to germinate.

Table 3. Percentage germination of *Lilium philippinense* bulbs and seeds from the different collection sites.

Population Sites	Latitude	Longitude	Elevation	Bulbs planted	Germinated bulbs surviving to flower (A)	Germinated bulbs not surviving to flower (B)	Total bulbs germinated (A+B)	% bulb germination (after 150 days)	No. of seeds sown	Germinated seeds	% seed germination (after 150 days)
Ambuklao, Indian	16.4728	120.7622	1042	6.00	2.00	0.00	2.00	33.33	210	81	38.57
Atok, Balangabang	16.5893	120.7586	1959	18.00	0.00	0.00	0.00	0.00	150	47	31.33
Atok, Topdak	16.5447	120.7132	1792	4.00	1.00	1.00	2.00	50.00	180	44	24.44
Atok, Halsema Rd.	16.6017	120.7640	2091	2.00	0.00	0.00	0.00	0.00	150	82	54.67
Bakun, Bagtangan	16.7476	120.7682	2058	9.00	0.00	0.00	0.00	0.00	90	34	37.78
Bauko, Lower Buga	17.0277	121.0922	2074	7.00	0.00	0.00	0.00	0.00	150	23	15.33
Bessang Pass	16.9728	120.6713	1292	29.00	6.00	0.00	6.00	20.69	300	130	43.33
Bokod, Bila	16.5531	120.8214	1481	7.00	0.00	0.00	0.00	0.00	270	101	37.41
Bokod, Bobok, Sawmill	16.4332	120.8551	1514	6.00	0.00	1.00	1.00	16.67	60	37	61.67
Bokod, Moatong	16.4755	120.8196	873	12.00	0.00	1.00	1.00	8.33	240	41	17.08
Bokod, Pito	16.4060	120.8649	1321	6.00	0.00	0.00	0.00	0.00	150	3	2.00
Bontoc, Bayyo	17.0158	121.0157	1276	10.00	2.00	1.00	3.00	30.00	30	0	0.00
Bontoc, Dantay	17.0777	120.9459	922	4.00	0.00	1.00	1.00	25.00	180	42	23.33
Bontoc, Gonogon	17.0459	120.9371	951	1.00	0.00	0.00	0.00	0.00	180	32	17.78
Bontoc, Km 388 Bon-Ban Rd.	17.0874	120.9544	911	10.00	3.00	3.00	6.00	60.00	210	10	4.76
Itogon, Ampucao	16.2844	120.6449	1353	14.00	1.00	4.00	5.00	35.71	120	86	71.67
Kabayan, Caleng, Bashoy	16.5712	120.8360	1085	1.00	0.00	0.00	0.00	0.00	60	6	10.00
Kabayan, Duacan	16.6140	120.8390	1232	12.00	0.00	3.00	3.00	25.00	150	16	10.67
Kapangan, Amunget	16.6489	120.6355	1066	13.00	0.00	3.00	3.00	23.08	30	21	70.00
Kayapa, Nueva Vizcaya	16.3576	120.8880	1103	2.00	0.00	0.00	0.00	0.00	150	24	16.00
Kibungan, Leseb, Sagpat	16.6695	120.6526	1324	2.00	0.00	0.00	0.00	0.00	60	35	58.33
Kibungan, Napsung	16.7332	120.6728	1291	13.00	0.00	1.00	1.00	7.69	30	0	0.00
Sabangan	16.9202	120.8928	1794	10.00	0.00	0.00	0.00	0.00	150	9	6.00
Sagada, Danom	17.0941	120.8856	1728	3.00	0.00	1.00	1.00	33.33	90	50	55.56
Sagada, after Danom	17.0950	120.8773	1685	5.00	1.00	2.00	3.00	60.00	90	7	7.78
Sagada, Madongo	17.1045	120.9130	1556	11.00	0.00	1.00	1.00	9.09	120	52	43.33
Samoki, Km 380 Bon-Ban Rd.	17.0849	120.9807	899	21.00	1.00	0.00	1.00	4.76	150	28	18.67
Tadian	16.9874	120.8417	1354	14.00	1.00	1.00	2.00	14.29	210	53	25.24
			Total	252.00	18.00	24.00	42.00	16.67	3960.00	1094.00	27.63

Table 4. One way analysis of variance (ANOVA) of the different variables.

		Sum of Squares	df	Mean Square	F	Significance
latitude	Between Groups	.047	3	.016	.191	.901
	Within Groups	1.956	24	.082		
	Total	2.003	27			
longitude	Between Groups	.037	3	0.012	.886	.462
	Within Groups	.336	24	0.014		
	Total	.373	27			
elevation	Between Groups	3735577	3	1245192.337	156.681	.000
	Within Groups	190735.1	24	7947.296		
	Total	3926312	27			
number of bulbs	Between Groups	152.730	3	50.910	1.233	.320
	Within Groups	991.270	24	41.303		
	Total	1144.000	27			
bulb germination	Between Groups	1502.604	3	500.868	1.491	.242
	Within Groups	8063.130	24	335.964		
	Total	9565.734	27			
number of seeds	Between Groups	3212.500	3	1070.833	.193	.900
	Within Groups	133330.4	24	5555.432		
	Total	136542.9	27			
seed germination	Between Groups	564.793	3	188.264	.366	.778
	Within Groups	12353.843	24	514.743		
	Total	12918.636	27			

Germination from seeds

Seed germination was observed and recorded after 150 days from sowing. Of the total 3960 seeds collected from the 28 population sites that were sown under greenhouse conditions, total seed germination was 27.63%. Of the seeds collected from the 28 population sites, the highest percentage seed germination was observed from Ampucao, Itogon with 71.67% germination. This is followed by seeds collected from Amunget, Kapangan, which showed a germination of 70%. In contrast, seeds collected from Bayyo, Bontoc and Napsung, Kibungan did not show signs of germination even after 150 days. Comparatively, the percentage seed germination in all the 28 populations showed variable percentages, from a minimum of 0% to a maximum germination of 71.67% (Table 3, Fig. 4). Nevertheless, despite the variable seed germination percentages, one way ANOVA showed that the number of seeds and the capacity to geminate did not significantly differ in the different population sites (Table 4).

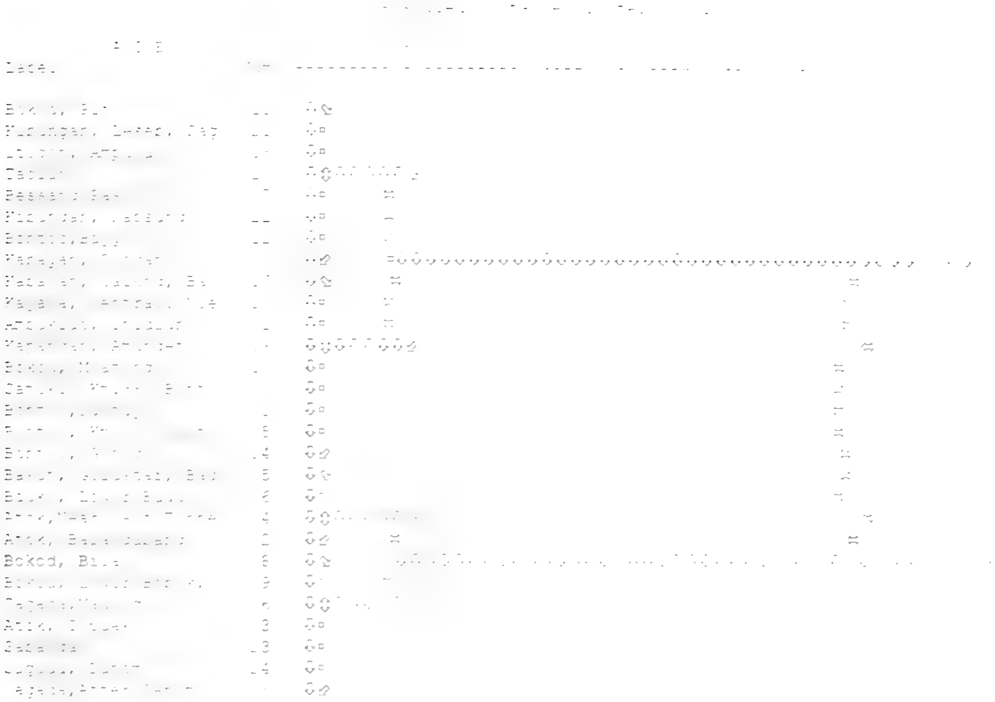

Fig. 3. Dendrogram of the population sites using hierarchical cluster analysis.

Generally, seed germination had a higher value of 27.63% relative to bulbs, which only showed a germination percentage of 16.67%. Across the 28 populations, seed germination was higher than bulb germination with few exceptions (Fig. 4). Additionally, in terms of seedling survival, despite the higher germination capacity from seeds, the plants remained as seedlings up to the third year. These seedlings did not reach maturity, unlike the sprouts from bulbs where 57.14% of the 16.67% that germinated survived until the flowering and fruiting stage.

To determine if there is a relationship among the percentage germination of seeds and bulbs across the 28 populations with respect to elevation and geographic origin, principal component analysis (PCA) was performed. Results showed that the 28 population sites had high loadings on the principal axis (Factor 1) with an *eigen* value of 99.89%. Furthermore, one way ANOVA shows that there were no significant differences among the number of seeds, percentage germination and collection sites. This demonstrates that elevation and geographic location of *L. philippinense* populations did not show significant variation in terms of their germinating capacity, both for the seeds and the bulbs.

Survival of plants from bulb and seed origin

The survival of plants originating from bulbs was observed over one year. Results showed that 57.14% of the 16.67% plants that germinated from bulbs were able to reach flowering stage. Almost half the seedlings from bulbs did not survive up to the

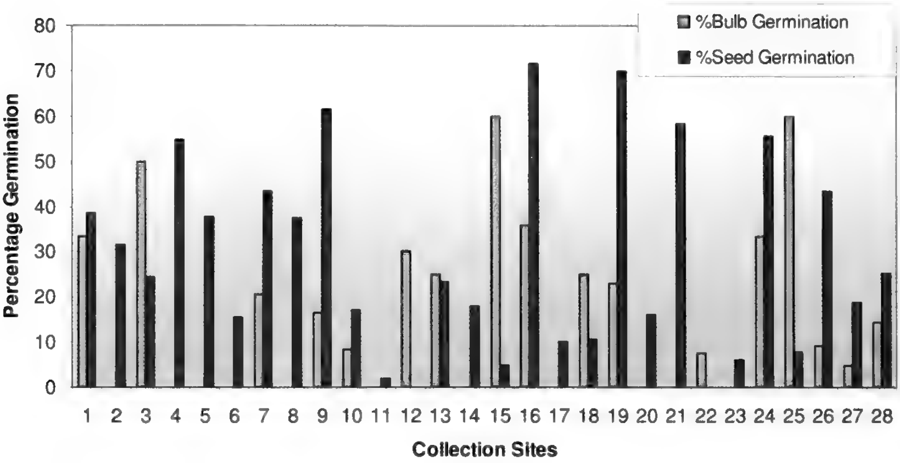

Fig. 4. Germination performance of *Lilium philippinense* bulbs and seeds from different collection sites. Collection sites: 1 Ambuklao, Inidian; 2 Atok, Balangabang; 3 Atok, Topdak; 4 Atok, Halsema Rd.; 5 Bakun, Bagtangan; 6 Bauko, Lower Buga; 7 Bessang Pass; 8 Bokod, Bila; 9 Bokod, Bobok, Sawmill; 10 Bokod, Moatong; 11 Bokod, Pito; 12 Bontoc, Bayyo; 13 Bontoc, Dantay; 14 Bontoc, Gonogon; 15 Bontoc, Km 388 Bon-Ban Rd.; 16 Itogon, Ampucao; 17 Kabayan, Caleng, Bashoy; 18 Kabayan, Duacan; 19 Kapangan, Amunget; 20 Kayapa, Nueva Vizcaya; 21 Kibungan, Leseb, Sagpat; 22 Kibungan, Napsung; 23 Sabangan; 24 Sagada, Danom; 25 Sagada, after Danom; 26 Sagada, Madongo; 27 Samoki , Km 380 Bon-Ban Rd.; 28 Tadian.

reproductive stage. This could perhaps be attributed to the presence of white aphids on the bulb-originated material during the observation period.

The plants that germinated from seeds demonstrated a peculiar characteristic. During the first year, these seedlings remained in their 2–4-leaf stage and wilted after eight months, leaving tiny bulbs that became dormant in the soil. In the second year, new sprouts developed from these tiny bulbs from the first year but these also remained vegetative, after which they again wilted without reaching reproductive stage, surviving once more as dormant bulbs in the soil. In the third year, sprouts again grew from 2-year-old bulbs, but also remained in a vegetative stage. Even at this particular stage, the bulbs had not reached their mature size (about 30–40 mm diameter).

Discussion

One of the most basic ways of propagating plants is through seed. For plants that develop both seed and bulbs such as lilies, seed germination has some advantages. First, it allows growers to propagate lilies that are difficult to obtain as bulbs. Second, seeds are usually disease and virus-free, even if they come from infected plants. Third, using seeds for propagation allows genetic variation in the succeeding population.

Germination from seeds is influenced by different factors such as dormancy, seed size, exposure to environmental factors and other factors that are inherent in the plant. Lily seeds have different types of germination depending on the species. *Lilium philippinense* exhibits an epigeal type of germination. In this study, seeds and bulbs of *L. philippinense* were exposed to a uniform set of environmental conditions in a greenhouse. There was low germination percentage for both seeds and bulbs. Lilies display a unique characteristic in terms of germination capacity. According to Elwes (1880), this is inherent to temperate species where germination from seeds in *Lilium* would show alternating dormancy and seedling initiation for three or more years. This period allows the bulblets to attain a functional size before it can finally grow into a reproductively active plant. Inherent dormancy was also demonstrated by Silvertown in 1999. He observed that Liliaceae species exhibit double seed dormancy. Two cold seasons are required for the seeds to fully germinate; the first cold stratification releases the radicle and the second releases the shoot so that the seeds require two years for germination. Related to this, some plant species have inherently low germination capacity even when exposed to suitable environmental conditions for germination. This observation was described by Lanta et al. (2003) for *Amaranthus cruentus* and *A. retroflexus*, which exhibit poor seed germination.

Studies of some species have shown that seed size often have significant effects on final germination percentage, seedling survival or seedling growth (Gross 1984, Navarro & Guitian 2003). Harper (1977) proposes that the poor performance of smaller seeds is due to their lower endosperm content. Seed germination in *L. philippinense* is possible to an extent of 27.63%; however, reproductive plants cannot directly grow from seeds. The plants that germinated from seeds wilted before reaching maturity but remained as tiny bulbs in the soil. This was also demonstrated in other studies (Schaal 1980, Dolan 1984, Marshall 1987, Naylor 1993). The size of the bulbs is an essential consideration owing to its capacity to store enough food materials to supply the seedlings the needed food during its development. Accordingly, the size of the bulb for commercial production of some lilies should range from 20 to 14 cm. In addition, plants grown from bulbs that are below 10 cm bears small and fewer flowers (Hermano 2000). In Benguet lilies, the size of the bulbs should reach an average of 30 to 40 mm.

In this study, bulb propagation in *L. philippinense* showed 16.67 % germination. This low germination percentage seems rather normal for some temperate species, even if the propagules were reared under optimal flowering conditions (Elwes 1880). In the present case, out of this percentage, only 57.14% developed until the flowering stage. Almost half of the germinated seedlings from bulbs died before reaching the reproductive stage, but it is not possible to know if the observed presence of aphids was a cause.

One important factor that determines the distribution and survival of a species is its ability to exist in harsh environments. In the case of *L. philippinense*, the 28 populations are part of a narrow distribution in the southern part of the CCR. This suggests that there is a suitable but restricted environmental condition for this species in this part of the CCR. The observation of horticulturists in the region that this species is difficult to cultivate outside of its natural habitat can be attributed to its specific and limited range of environmental requirements.

Conclusions

The fact that germination from seeds and bulbs can be obtained despite its limited extent demonstrates that it is possible to propagate *L. philippinense* using bulbs and seeds outside of their natural environment, provided that optimal environmental conditions will be met.

However, in conservation terms, germination from bulbs and seeds are just two techniques for propagating material. Other faster means of propagation, like tissue culture, have yet to be explored for *L. philippinense*. With declining populations of this species, it is essential and interesting that proper and efficient ways of rapid multiplication of material should be considered in future studies.

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Predicting distribution of *Lilium philippinense* (Liliaceae) over Luzon's Cordillera Central Range, Philippines, using ArcGIS Geostatistical Analyst

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ABSTRACT. The growing importance of geographical information system (GIS)-based output in the analysis of biodiversity data is due to its convenient method of spatial analysis of data and prediction of plant geographical distribution. The Interpolated Distance Weight Method (IDW) of ArcMap ArcGIS 9 was used to determine possible areas of *Lilium philippinense*, endemic to the Cordillera Central Range (CCR) and declining in population due to habitat destruction, swidden activities and over-collecting. The variables considered in this study are soil pH, soil phosphorus content, organic matter, elevation, latitude and longitude. All variables were studied from actual *L. philippinense* sites and, using IDW, prediction maps were generated that identified areas where *L. philippinense* are likely to thrive. The Geostatistical Analyst of ArcGIS is a useful tool for predicting potential sites for introduction of *L. philippinense* as an extended *in-situ* conservation strategy.

Keywords. ArcGIS, Cordillera Central Range, distribution prediction, *Lilium*, Luzon, Philippines, potential geographic distribution

Introduction

The study of plant species distribution is an important aspect of biodiversity science. Currently, modeling distribution is less taxing with the use of computer applications or software. If modeled visually through maps, data taken from the field can be interpreted and analysed more accurately. Geographic Information System (GIS) software, specifically, ArcGIS 9, provides storage of quantitative data for generating visual representation on a geographic reference, and retrieval and analysis of information (Fischer 2009). According to Main et al. (2004), GIS help manage, analyse, and present spatially related information combining multiple layers of environmental and biological information related to a spatial location, to gain a better understanding of a specific location (Main et al. 2004). Additionally, researchers can use GIS to fully investigate data and develop spatially accurate graphical data displays. This is very important, especially in geographic distribution where a more accurate and graphical display of populations can be presented. This graphical display can help in decision-making, such as in conservation. This paper focuses on the use of the

Interpolated Distance Weight Method (IDW) in the interpolation of known data of *Lilium philippinense* Baker (Liliaceae) population sites to predict potential areas for cultivation.

In ArcMap, a data layer can be created for each variable of the observed sites. ArcMap is a map-centric application that supports editing and viewing of maps (Longley et al. 2005) and used in visualising different types of data providing an interactive interface for data manipulation, information retrieval and spatial analysis (Zeiders 2002). A data layer is generated from a database of the values of the variables, with the longitude and latitude of the sites. Each data layer can be used by the IDW method of ArcMap GIS to produce the prediction maps. The prediction map is another layer which predicts the values of the predicted sites and compares it with the other areas of unknown data.

The distribution of *L. philippinense* populations was addressed in this study because, first, it is an endemic species in the southwestern part of the Cordillera Central Range (CCR); second, its populations are already declining due to anthropogenic activities; third, few studies have documented this endemic species; and fourth, a dataset consisting of variables such as latitude, longitude, elevation, and soil parameters such as soil pH, phosphorus and organic matter content has been gathered by Balangcod (2009) and allowed to be used in this study. These variables were used to create data layers using ArcMap GIS 9. Specifically, the dataset was used to predict the potential sites of distribution of *L. philippinense* in the CCR using the IDW method of ArcMap GIS 9. With the population of *L. philippinense* dwindling, the use of a dataset in extrapolating and predicting potential sites for the introduction of the species in an extended *in-situ* conservation programme is helpful.

In using the GIS software, a fair knowledge of computers is a necessity as some parts of the software call for critical analysis, an element taught in computer science.

The features and uses of ArcGIS

GIS is defined by Paul Longley et al (2005) as a computerised tool for solving geographic problems, a mechanised inventory of geographically distributed features and facilities, and a tool for performing operations on geographic data that are too tedious or expensive or inaccurate if performed by hand. Childs (2004) describes GIS as all about spatial data and the tools for managing, compiling and analysing that data. GIS has numerous uses such as census, mapping, modelling and prediction.

ArcGIS is a leading software in the GIS market due to its extensive features and global community of users (Information Management Editorial Staff 2004). Among its features is the interpolation tool in the Spatial Analyst extension. Interpolation is a process used to predict the values of cells at locations that have no information. Using the principle of spatial autocorrelation which measures the degree of dependence between near and distant objects, interpolation determines interrelation of values to also determine the spatial pattern (Childs 2004). Another principle which is the basis of spatial interpolation is Tobler's Law, which states that "all places are related but nearby places are more related than distant places" (Miller 2004). This means that the best guess for a point with no information is the value measured at the nearest observation points (Longley et al. 2005).

Another interesting feature of ArcGIS is the use of interpolation methods such as IDW, Kriging and Spline. The IDW method is a deterministic interpolation technique. Deterministic interpolation uses mathematical formulas or measured points to create surfaces (Childs 2004). Kriging is a popular statistical method based on regionalised variables (Longley et al. 2005) and Spline is a method that uses a mathematical function that minimises overall surface curvature (Childs 2004). IDW is the method most often used by spatial analysts due to its simplicity. It estimates unknown data by getting the average of known measurements of nearby points, with the nearest neighbours getting greater weight in the computation of averages. The formula used by IDW is as follows:

$$z(x) = \sum_i w_i z_i / \sum_i w_i$$

where x is the point of interest, the unknown value is denoted by $z(x)$ and the known measurements as z_i. The weights (w_i) are defined most often by the inverse square of distances formula:

$$w_i = 1 / d_i^2$$

where d_i is the distance from x to x_i, with x_i as the points where measurements were taken. The data points run from 1 to i. (Longley et al. 2005).

Almost all information that requires mapping or modelling over the Earth's surface can now be effectively stored and retrieved using Information Systems. Specifically, Geographic Information Systems or GIS are used for these tasks. In recent years, modelling potential species distributions using GIS has become popular because it is a powerful tool for researchers involved in vegetation mapping, biodiversity mapping and population distributions (Moreno et al. 2007, Murray 2009, Hasmadi 2010). GIS is also a convenient tool in creating prediction maps (Pallaris 1998, Sergio & Draper 2002, Vargas et al. 2004, Vogiatzakis & Griffiths 2006). The last-mentioned study modeled the potential distribution of 36 endemic and 47 non-endemic species of *Anthurium* (Araceae) in Ecuador based on mean annual temperature and humidity. GIS was also used to identify and analyse the environmental tolerance limits of *Cecropia* (Pallaris 1998).

Methodology

Study area

The Cordillera Central Range (CCR) is located in the northern part of the Philippines. It is a mountainous region, with an estimated total area of 17,500 km (CPA Phil. 2006). It has six provinces, viz., Apayao, Abra, Mt. Province, Ifugao, Kalinga and Benguet. The CCR has a diverse flora and fauna, some of which are endemic to the area. *Lilium philippinense*, a species described in 1880, is endemic there (Elwes 1880).

Lilium philippinense is one of three species of *Lilium* L. found in the CCR (Palima 1988). It is a bulb species with a strikingly white trumpet-like flower. The flower has an aromatic fragrance and is produced singly per stem. Each plant bears 1–2, rarely to 4, stems. This species flowers only once per year and is visible during the rainy season from late May to August (Balangcod 2009).

Between 2007 and 2009, a study indicated 118 population sites of *L. philippinense.* These sites were georeferenced using a GPS receiver, Garmin's GPSmap 60C, where latitude, longitude and elevation were recorded. Out of the 118 sites, soil samples from 45 sites were collected for determining the soil pH, phosphorus and organic matter content. These additional variables together with the longitude, latitude and elevation were used with the IDW of ArcMap Gis 9 to predict potential sites where *L. philippinense* would likely grow.

Two sets of data were used. The first set comprises data on latitude, longitude and elevation taken from 118 sites, and the second data set comprises data on latitude, longitude, elevation, soil pH, phosphorous and organic content taken from 45 sites that were a subset of the 118 sites mentioned. All data gathered from the fieldwork was initially saved in excel files (.xls) but were converted to database files (.dbf) since it is the format needed by ArcMap to plot the data on the map.

Using the four characteristics: elevation, soil pH, phosphorous and organic matter, four colour-filled contour prediction maps were produced. These four maps were overlain on the CCR map to determine the areas where *L. philippinense* Baker is predicted.

Preprocessing

A base map for plotting the data was needed for visualisation in ArcMap. A vector and raster dataset of the Philippine map with provincial boundaries was taken from PhilGIS, a website that provides free Philippine spatial data. Separate maps for each province with municipality boundaries were also obtained from the same website. The Philippine maps in shapefile format (.shp) were set in ArcMap using its default datum World Geodetic System (WGS) of 1984 as its coordinate system which is also the datum used in all layers of data in ArcMap.

Use of GIS in predicting sites for Lilium philippinense

Modelling the distribution of different sites across the CCR employed the two data sets mentioned. Prediction maps were generated for each factor: elevation, soil pH, phosphorous and organic matter content of the soil. The Spatial Analyst IDW was used to generate prediction maps with settings of the default power of two. This power value controls the significance of known points on the interpolated values, based on the distance of the known and the output points. Higher values of power may cause "non-smoothness" of values (Longley et al. 2005). The number of nearest neighbours was set to 15, meaning computation of the unknown data depends on the nearest 15 known data.

Using IDW interpolator, the ArcMap calculates the value of each cell of the map depending on the weight or attributes of its neighbouring data. Given that the observed data were randomly distributed in the CCR, the Variable option was used under the search option (Longley et al. 2005).

Verification

To verify the accuracy of the prediction, specifically the prediction maps for the elevation, a Digital Elevation Map (DEM) was downloaded and was used to cross-check the predicted values against the true values. The presence of the DEM allows comparison of the predicted and the actual values.

For the prediction map for elevation using the 45 study sites, 60 sample areas from the predicted sites were chosen randomly for verification. Ten areas were chosen from each province (Fig. 1). Variables such as latitude, longitude, and elevation for these areas were extracted from the DEM and then compared with the predicted elevation.

To verify further, the GPS readings of the elevation of 33 population sites that were included in the 118 study sites but excluded from the subset of 45 study sites were also noted. These 33 sites or points were found within the coloured contours of the prediction map. Note that the 118 sites and the subset of 45 sites have elevation data gathered from the field survey using a GPS handset.

As for the prediction map for elevation using the 118 study sites, the same 60 sampling areas were used and the actual and predicted elevations noted. The percentage errors for the predictions using only a subset of 45 study sites and using the full complement of 118 study sites were computed and compared.

Results

Spatial analyst – IDW method

There were four data layers used in this study. The first type comprised the shape files for the six provinces of the CCR Region: Abra, Apayao, Benguet, Kalinga, Mt. Province and Ifugao which have data until the municipal level. The second type was a Philippine Digital Elevation Map (DEM) which had the actual elevation for the entire country. The third data layer was made up of the corresponding latitude and longitude of the study sites. Finally, the prediction maps generated by the Spatial Analyst of ArcMap constituted the fourth data layer.

The *first data layer* was taken from PhilGIS, a website that provides free shape files for the Philippines. There are six shape files, all with boundaries until the municipal level. The shape files have information including province, municipal or town and barangay. The *second data layer* was taken from a GTOPO30 website. This layer was a raster component which stored the elevation value for each latitude and longitude coordinate of the Philippines. The *third data layer* comprised the two datasets

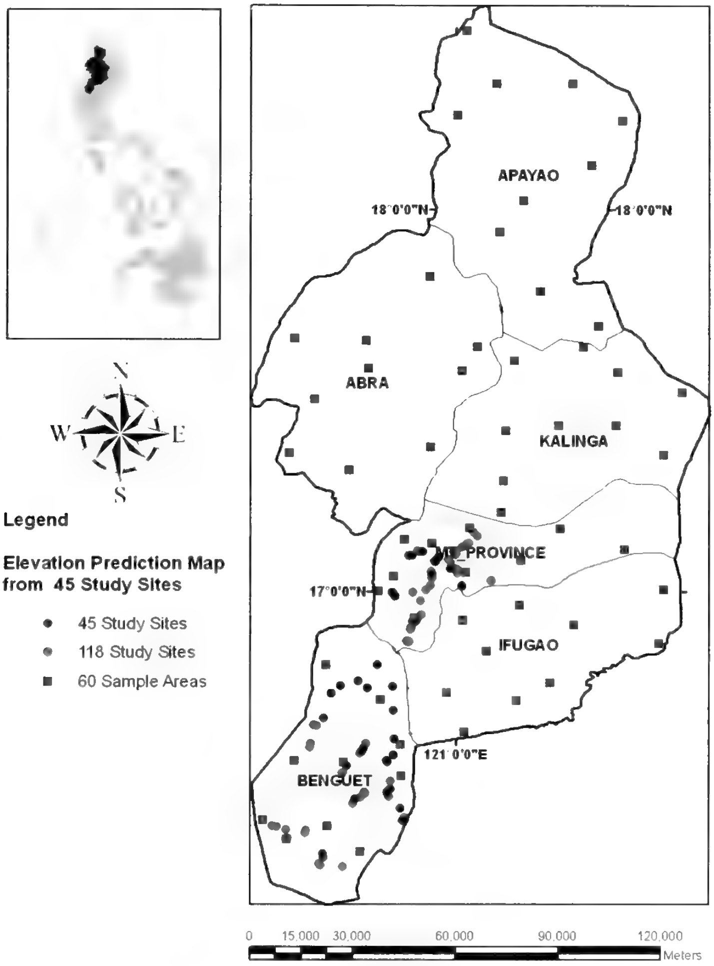

Fig. 1. Sixty sampling areas were randomly chosen to verify the predicted values of elevation generated from the prediction maps that used data from just 45 sites, and all 118 sites. The 45 sites mentioned are a subset of the 118 sites.

taken from the 118 study sites and the subset of 45 study sites. Each dataset had its own separate layer. These layers were superimposed on the others. These study site layers were derived from the table initially saved in Excel format (.xls) that was later changed into a database file (.dbf). The data needed for plotting were latitude, longitude and elevation. The *fourth layer*, consisting of the prediction maps, was generated by the ArcMap IDW Interpolator. There were five prediction maps produced. Two prediction maps using the elevation were created from the subset of 45 sites and from the full complement of 118 sites (Fig. 2 and 3). The other three factors, soil pH, phosphorous content of soil and organic matter were the input used for the other three prediction maps (Fig. 4 to 6).

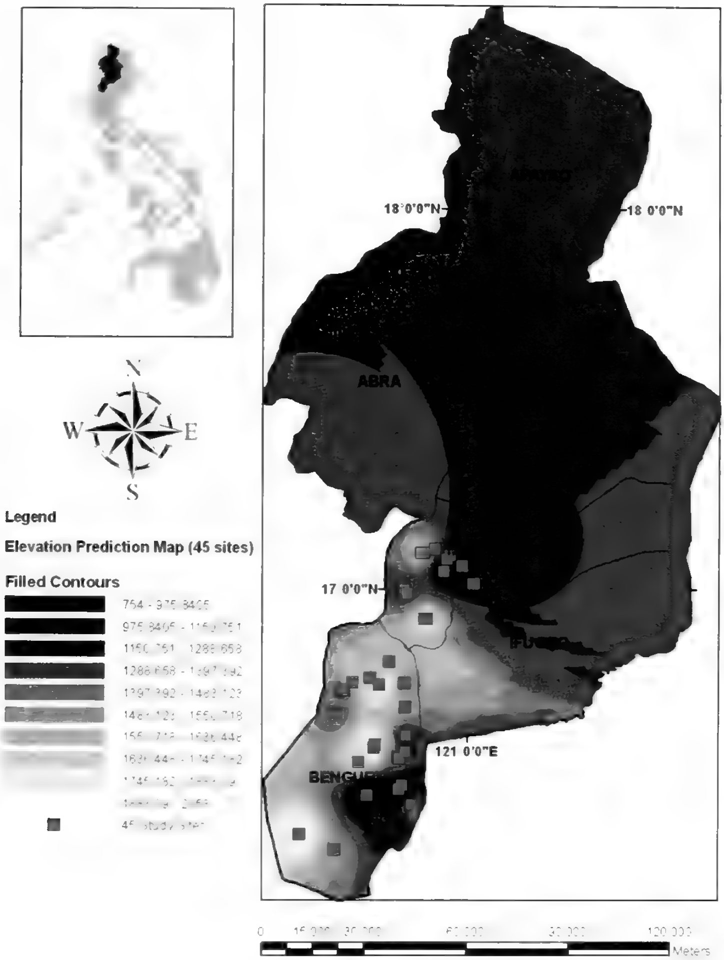

Fig. 2. Prediction Map using elevation of 45 observed sites of *Lilium philippinense*.

However, the ArcMap Spatial Analyst IDW method of prediction uses only values within the range of known data in predicting the values for areas that have unknown data. For example, if the known data are 0, 5, 7 and 10, then unknown data will only have a value within the range of 0 to 10. In this case, the predicted elevation of the unknown areas would only have a predicted value within 754 to 2058 m, when data from only 45 sites were used, and a range of 754 to 2155 m when data from all 118 sites were used. The same applies to prediction of the other factors, namely, soil pH, phosphorous content and organic matter.

To delimit the area of prediction, the range of values where the most number of sites were found was determined. For example, the elevation ranges of 754 to 2058 and 754 to 2155 were divided into ten classes. ArcMap automatically divides the ranges with the specification of the number of classes as input. The top five ranges or 50% of the ranges with the highest number of sites were noted for each data set and

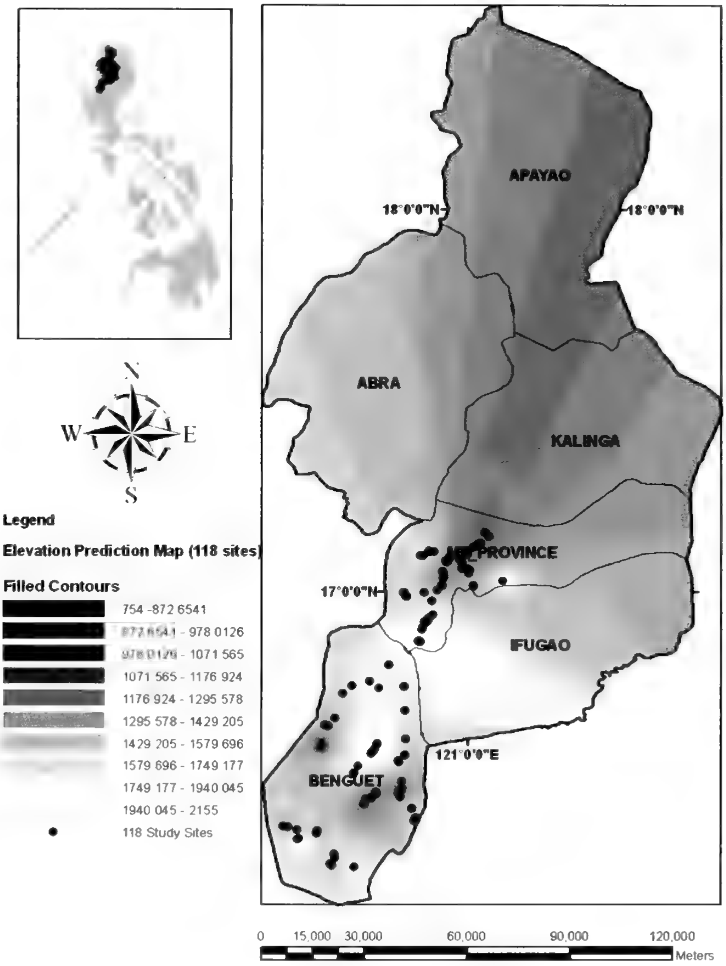

Fig. 3. Prediction Map using elevation of 118 observed sites of *Lilium philippinense.*

were the only data visible in the prediction maps. Table 1 contains the values for the ranges and the corresponding number of sites for each range. Separate prediction maps were created for both sets.

For data on soil pH, phosphorous content and organic matter, their ranges were also divided into ten classes each, and the top five ranges where the most number of sites were found were noted and mapped.

After creating the prediction maps, merging of all maps using all factors (elevation, soil pH, phosphorous content and organic matter) was done and the areas where *Lilium philippinense* was predicted to thrive was determined. This is inferred from the overlain map. The Identify Tool of ArcMap enables a point-and-click query of the location using the shape files of the six provinces.

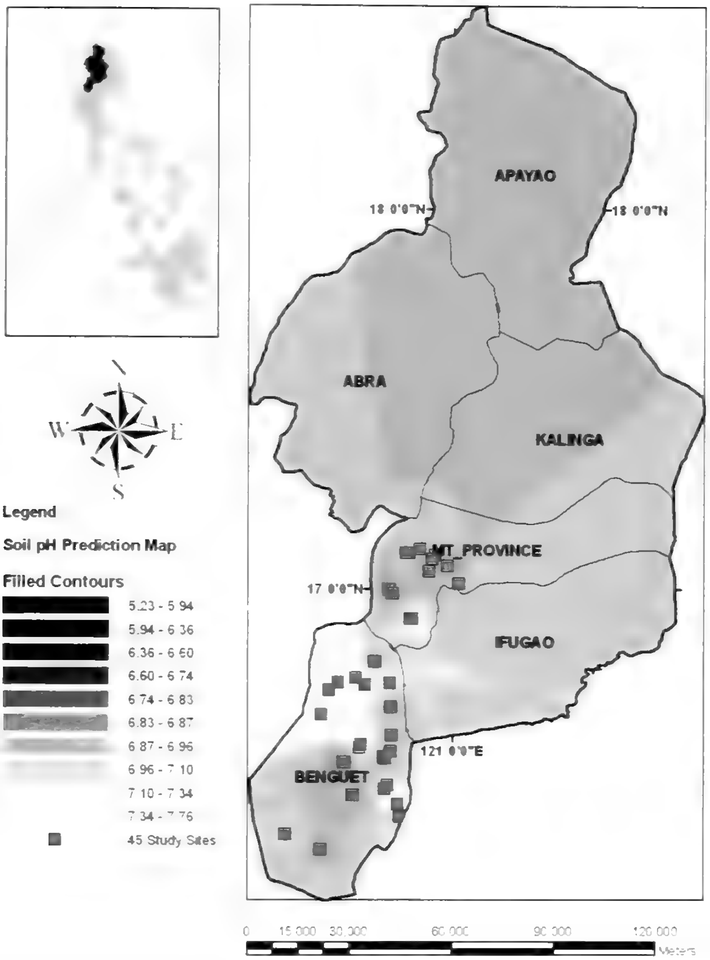

Fig. 4. Prediction Map using soil pH generated from 45 observed sites of *Lilium philippinense*.

There were two output maps from the merging of all prediction maps. The first used the three prediction maps of soil pH, phosphorous content of soil and organic matter with the elevation prediction generated from the subset of 45 study sites. The second map used the same three prediction maps but merging with the elevation map from all 118 sites, instead of from just 45 sites. The areas where the four prediction maps overlap were highlighted in black and isolated.

Percentage Error

Elevation is the factor that can be verified using actual measured GPS values and the DEM. Prediction of elevation generated from 45 study sites, or 45 known points, was computed against the actual values taken from the DEM and was compared with the prediction of elevation generated from 118 study sites. From the 60 sample areas, the elevation from both the predicted elevation generated from 45 study sites, and the

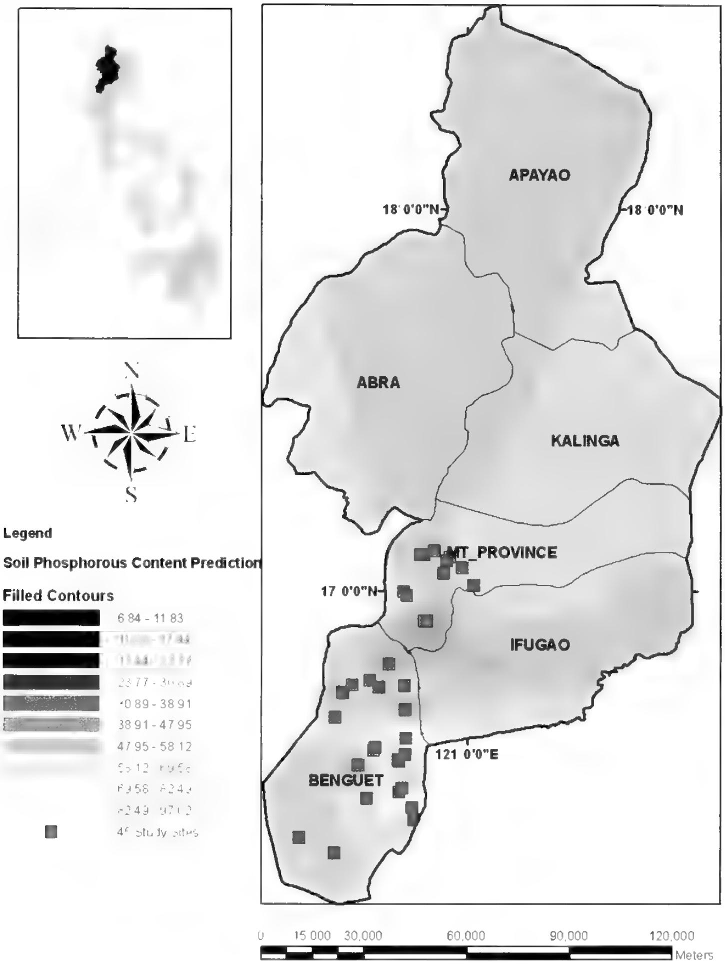

Fig. 5. Prediction Map using phosphorous content of soil generated from 45 observed sites of *Lilium philippinense*.

predicted elevation generated from 118 study sites, were recorded and the percentage error computed. Using the formula below, there is a percentage error of 68.57% for the 45 study sites while the 118 sites had only 47.16% error.

$$\left(\frac{actual - predicted}{actual}\right) * 100$$

The prediction generated from the 45 study sites was further verified by computing the percentage error with GPS readings from the 118 sites. The elevation of 33 random sites not included in the 45 sites were used as the actual value. The percentage error was 7.99%. However, if the DEM of the 33 sites were used as actual values, the percentage error was only 4.31%.

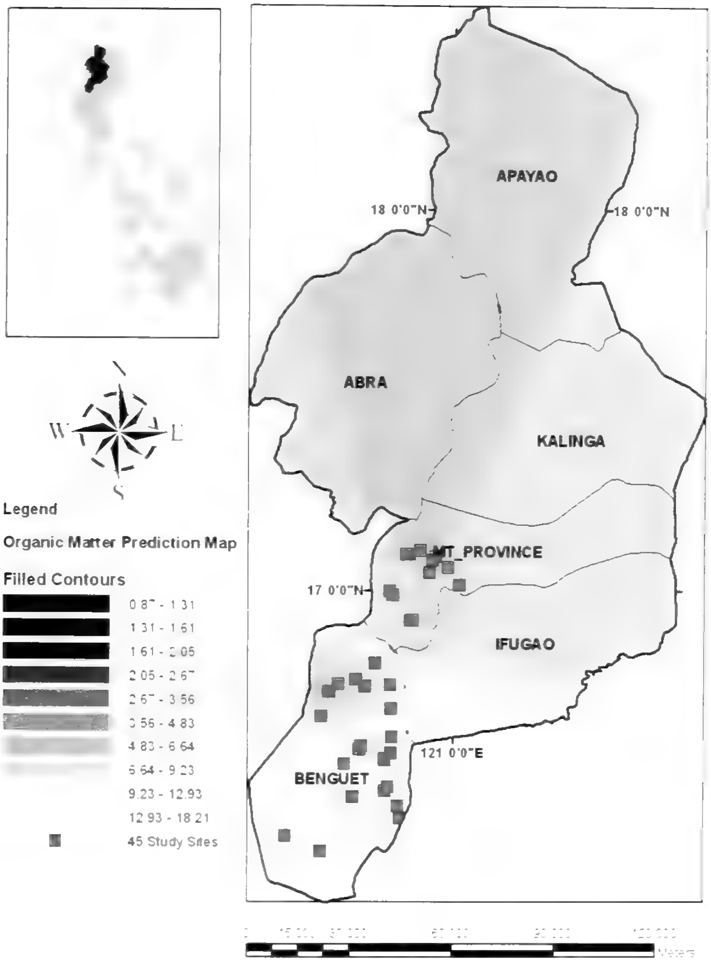

Fig. 6. Prediction Map using organic matter generated from 45 observed sites of *Lilium philippinense*.

From the merged predicted maps of elevation, soil pH, and phosphorous content of soil, a list of predicted municipalities were identified using the Municipal maps taken from PhilGIS website. The areas are given in Table 2.

Discussion

The ArcGIS ArcMap creates a good visualisation of data geographically. It allows modelling of the locations of where *L. philippinense* were observed for users to easily identify the sites and the similarity of sites. This was shown in the different maps produced.

Table 1. Ranges for elevation, soil pH, soil phosphorous content, organic matter and the number of study sites located within each range. * denotes ranges used in the final prediction mapping. 50% of the ranges with the highest number of study sites were taken into account.

Attribute	Range	No. of Study Sites	Range	No. of Study Sites
Elevation (45 sites)	754.0000–975.8405	7*	1483.230–1550.718	4
	975.8405–1150.751	6*	1550.718–1636.448	2
	1150.751–1288.658	5*	1636.448–1745.182	6*
	1288.658–1397.392	5*	1745.182–1883.090	2
	1397.392–1483.123	3	1883.090–2058.000	5
Elevation (118 sites)	754.0000–872.6541	10	1295.578–1429.205	9
	872.6541–978.0126	19*	1429.205–1579.696	14*
	978.0126–1071.565	13*	1579.696–1749.177	10
	1071.565–1176.924	9	1749.177–1940.045	9
	1176.924–1295.578	13*	1940.045–2155.000	12*
Soil pH	5.23–5.94	3	6.83–6.87	3
	5.94–6.36	4*	6.87–6.96	3
	6.36–6.60	9*	6.96–7.10	3
	6.60–6.74	3	7.10–7.34	8*
	6.74–6.83	4*	7.34–7.76	5*
Soil phosphorous content	6.84–11.83	7*	38.91–47.95	5*
	11.83–17.44	4*	47.95–58.12	5*
	17.44–23.77	5*	58.12–69.58	4
	23.77–30.89	4	69.58–82.49	3
	30.89–38.91	4	82.49–97.02	4
Organic matter	0.87–1.31	5*	3.56–4.83	5*
	1.31–1.61	6*	4.83–6.64	6*
	1.61–2.05	4	6.64–9.23	1
	2.05–2.67	4	9.23–12.93	4
	2.67–3.56	8*	12.93–18.21	2

Table 2. Identified municipalities under each province where *Lilium philippinense* was predicted to grow.

Province	Municipalities
Abra	Bangued. Danglas. Langiden. La Paz. Luba. Penarrubia. Pilar. San Isidro. San Quintin. Villaviciosa
Kalinga	Balbalan. Lubuagan. Pinukpuk. Tabuk. Tanudan. Tinglayan
Apayao	Conner
Mt. Province	Bontoc. Sadanga. Sagada. Tadian
Ifugao	Asipulo. Lagawe. Lamut. Tinoc
Benguet	Atok. Bokod. Buguias. Itogon. Kabayan. Kapangan. La Kibungan. Trinidad

The Spatial Analyst IDW was able to predict the values of unknown data given the actual points. However. the limitation of the IDW method. that did not produce values other than the specified range of the known data. has a huge effect on the accuracy of values. The output of the prediction cannot generate values higher or lower than the observed or known values. A possible solution is to acquire more data in sites. not necessarily where *Lilium philippinense* is observed. especially in places on the northern part of the CCR Region. A wider spread of range of values and location would perhaps enable better prediction.

In addition. the IDW method in interpolation to generate prediction maps is based on proximity. and its accuracy in giving a good prediction depends on the number of actual values surrounding that empty space or grid on the map. The nearer and the more the actual values are to an empty space or grid. the better the prediction for that space. This means that if the actual values were found in one specific area. the correctness of the prediction grows less with farther distance (Longley et al. 2005). Due to this limitation of the IDW. prediction is more accurate for areas nearer the observed sites. In this study. the extent of the prediction maps were set to the boundaries of the whole CCR. hence. predicted areas that were farther relative to the actual distribution may not be accurate.

The presence of the majority of known points in the southern part of the CCR Region also affects the prediction. The IDW relies greatly on distance. and therefore the farther the distance of the unknown area from the area with known data. the lower the chances for a good prediction. This is validated with the result of the percentage error of the prediction from the 45 study sites.

Conclusions and recommendations

GIS is a very useful tool in plant distribution. Specifically, the IDW feature of ArcGIS is useful in predicting potential sites for cultivating endangered species like the *L. philippinense.* The accuracy of prediction is dependent on available data and the number of points (populations) that are plotted on the map. The more data and points, the more accurate is the prediction.

The data provided for *L. philippinense* is still limited. Factors such as air temperature and rainfall were not included in the prediction maps since there were no complete measurements for the whole region. There are only three weather stations located in the CCR and these stations are located in Baguio City and Benguet province.

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Towards the conservation of Malaysian *Johannesteijsmannia* (Palmae)

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ABSTRACT. A total of 20 new localities were recorded for the genus *Johannesteijsmannia* since 1972, demonstrating that the genus is less restricted in its distribution in Malaysia than previously thought. Nevertheless, *Johannesteijsmannia* is regarded as threatened with *J. lanceolata*, *J. magnifica* and *J. perakensis* assessed as endangered and *J. altifrons* as vulnerable. Endangered status was given to endemic species with restricted occurrence and small population size found in less than five localities. Recommended conservation measures include the need to expand *in situ* protection for populations in vulnerable habitats, inclusion of the species into forest management plans, and establishment of a sustainable seed harvesting regime. We also suggest regular monitoring of populations situated along forest boundaries and initiation of long-term conservation biology research. Habitats at risk in Jerantut-Benta (for *J. lanceolata*), Serendah and Bukit Kinta Forest Reserves (for *J. magnifica*), and Perak, i.e., Bintang Hijau, Kledang-Saiong and Bubu Forest Reserves (for *J. perakensis*) should be given protected status and *ex situ* conservation should be implemented.

Keywords. Conservation, extent of occurence, *Johannesteijsmannia*, red list, threat assessment

Introduction

Johannesteijsmannia is a small genus with only four species, i.e., *Johannesteijsmannia altifrons* (Reichb.f. et Zoll.) Moore, *J. magnifica* J.Dransf., *J. lanceolata* J.Dransf. and *J. perakensis* J.Dransf. (Dransfield 1972). All species are endemic to Peninsular Malaysia except *J. altifrons*, which is distributed from south Thailand to Peninsular Malaysia, Sumatra and Borneo. The genus is threatened (Walter & Gillett 1998), and seed harvesting for the ornamental plant trade contributes to its decline (Chan & Saw 2009).

Since Dransfield (1972), many new localities of *Johannesteijsmannia* have been recorded based on herbarium collections and field observations. The known extent of occurrence or distribution range in Malaysia for these species has thus greatly increased. *Johannesteijsmannia* is found in tropical lowland moist forest and lower montane forest, and the rapid change in land use patterns of such forests in the peninsula in the last decades of the 20th century had caused further loss of habitat and populations. This land use pattern had, however, slowed down significantly since the early 1990s and the time is now ripe to re-assess the conservation status of its species as more data on habitat status, population sizes, reproductive biology, and uses (Chan & Saw 2009) are available.

Here, we present the results of the threat assessment and discuss pertinent issues regarding the conservation of *Johannesteijsmannia*. We also recommend conservation and management measures for species which are threatened.

Materials and methods

Members of the genus were assessed following guidelines outlined in the Malaysia Plant Red List Guide for Contributors (Chua & Saw 2006) using the IUCN Red List Categories and Criteria version 3.1 (IUCN 2001). For each species, a map of its extent of occurrence (EOO) and area of occupancy (AOO) was prepared based on specimens lodged at the Kepong Herbarium (KEP) and the Sarawak Herbarium (SAR). This genus is absent in Sabah, hence there was no attempt to collate records lodged at the Sandakan Herbarium (SAN). Field observations and localities cited by Dransfield (1972) and Look (2007) were included. The EOO and AOO were calculated using the extensions Crime Analysis Tool 2.E and Conservation Assessment Tools (CATS) version 1.2 for ArcView GIS 3.2a, respectively. In assessing habitat decline for Peninsular Malaysia, we referred to the forest cover data based on the National and State Forest Inventories and land use data (MACRES & UTM 2008). Recent forest cover and land use data from Sarawak, however, were unavailable for use.

Results

Since Dransfield (1972), a total of 20 new localities were recorded for *Johannesteijsmannia*, with new records for Terengganu (*J. altifrons*) and Kedah (*J. perakensis*) (Fig. 1). *Johannesteijsmannia altifrons* is far more commonly distributed than once thought, especially in the east of the peninsula, with the majority of the populations occurring in Terengganu and Johor. The collection from Temengor Forest Reserve (FR) is a new record for Perak. With 16 additions of new localities since 1972, the EOO and AOO have dramatically increased for *J. altifrons* (Table 1). This species commonly inhabits valleys and hill slopes with lowland and hill dipterocarp forests on well-drained soils. It also grows at elevations of 1000–1200 m in the lower montane forests of Taman Negara, i.e., Gunung Tahan and Gunung Mandi Angin (Dransfield 1972). The population in Jerangau, Terengganu grows on waterlogged sandy soil in low-lying areas. The habitat of *J. altifron*s in the peninsula now seems more general and diverse than previously thought. In Sarawak, it is confined to the heath forests (Dransfield 1972) in sheltered valleys.

Similarly, *J. lanceolata, J. perakensis* and *J. magnifica* which were thought to be narrowly distributed endemics, now have wider distributions with new records from Negeri Sembilan, Kedah and Perak, respectively. They are found in sheltered hill slopes and valley bottoms, and are almost absent on ridges. One population of *J. magnifica* in Bukit Kinta FR, Perak, was recorded from a limestone area.

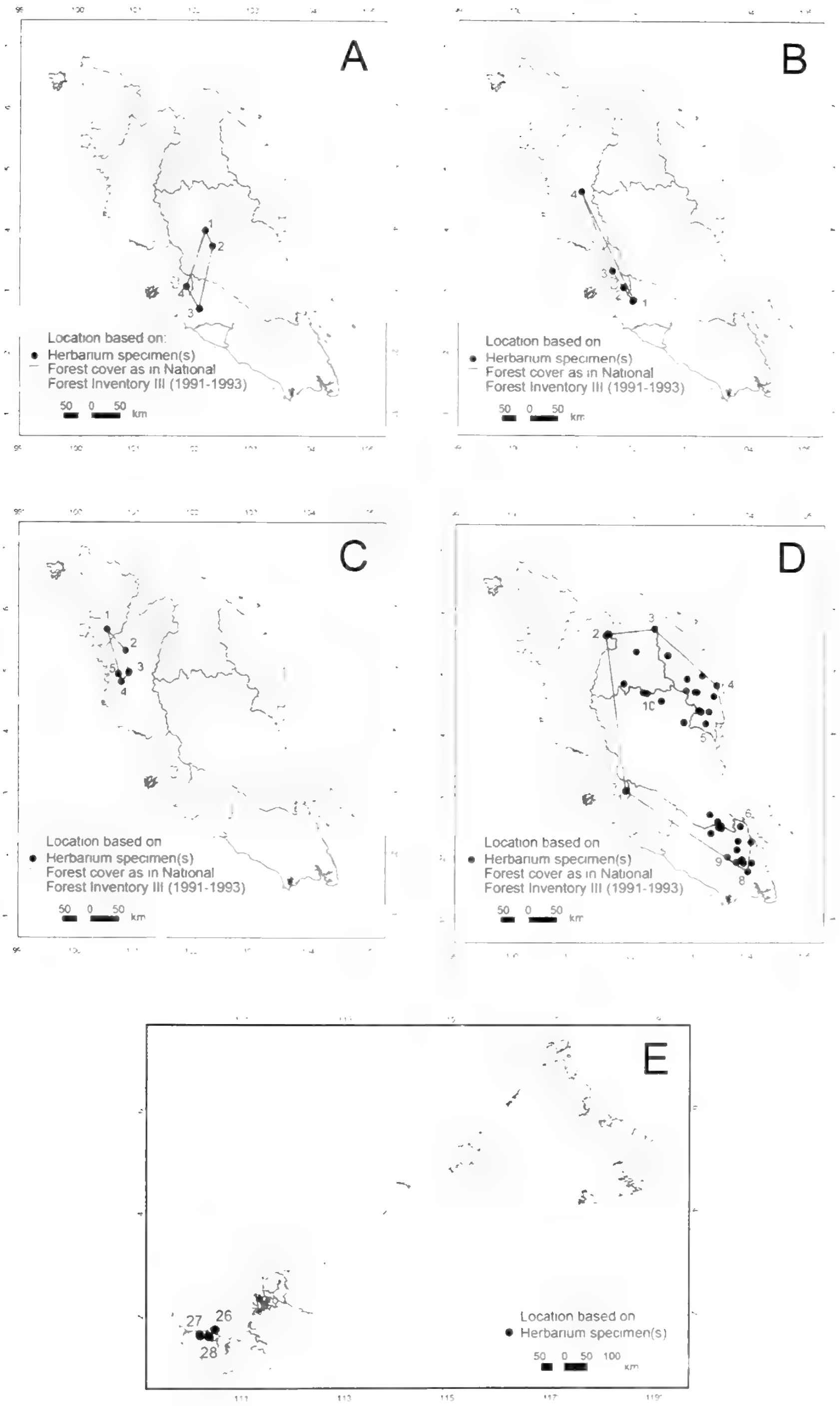

Fig. 1. Distribution of *Johannesteijsmannia* in Malaysia. **A.** *J. lanceolata*. **B.** *J. magnifica*. **C.** *J. perakensis*. **D–E.** *J. altifrons*. Polygons represent Extent Of Occurrence (EOO). See Appendix A for locality details. National Forest Inventory, NFI III information in A–D courtesy of Forest Department, Peninsular Malaysia.

Table 1. Threat assessment of *Johannesteijsmannia* based on extent of occurrence (EOO) and area of occupancy (AOO) following the IUCN Red List Category and Criteria ver 3.1 (2001).

Species	EOO (km^2)	AOO (km^2)	Category	Criteria
Johannesteijsmannia altifrons	58,804	176	VU	A4acd, C1
J. lanceolata	2,783	16	EN	A4acd,B1ab(ii,iii), C2a(i)
J. magnifica	1,306	16	EN	B1ab(ii,iii,iv), C2a(i)
J. perakensis	1,309	20	EN	A4acd,B1ab(ii,iii,iv),C2a(i)

The genus is considered threatened, with three species endangered and one vulnerable (Table 1). Populations of all species have declined or are declining due to deforestation and dam construction, and the possibility that seed harvesting for the ornamental trade could be a damaging factor requires to be better studied (Chan & Saw 2009). *Johannesteijsmannia lanceolata, J. magnifica* and *J. perakensis* qualified for the endangered category because they are endemics with restricted EOO and small population sizes (with less than 250 mature individuals in the largest subpopulation).

Generally, *Johannesteijsmannia* spp. are gregarious but with patchy distribution and probably limited dispersal ability. It is common to find populations confined to a single hill or valley. Because the populations are so restricted, they are extremely vulnerable to extinction. Clearly, any major catastrophe or destruction of a single site is likely to wipe out the entire subpopulation. Although many new localities have been added since 1972, the forest structure and quality in these sites and in sites predating the Dransfield's (1972) account have declined significantly. The species favour pristine sites in the lowland forests and many of these sites, with the exception of those in the National and State Parks, are no longer as pristine.

Populations located in the production forests of the Permanent Reserved Forests (PRF) network are not spared from logging damage. The creation of large gaps in the forest canopy and the disintegration of forest structure during logging could harm *Johannesteijsmannia*, either by direct physical damage or physiologically. We have examined a *Johannesteijsmannia* population in a logged-over forest of Berembun FR and found that these palms are apparently failing to regenerate as juveniles are rare.

A few localities are within water catchment areas where no logging is allowed and these populations are considered safe. Some of these populations, e.g., in Sungai Lalang, Tembat and Linggiu, are now remnants of an originally larger population, after dams were built. Only a handful of populations are in the totally protected areas of the National and State Parks and Wildlife Reserve.

While most of the populations are located within the PRF, some occur in state lands (Appendix A). A state land is land bank set aside by a state government to accommodate future development. Populations that occur on state lands are thus highly vulnerable to extermination. For example, the site of *J. altifrons* in Semariang Road has probably been developed into a town. The population of *J. lanceolata* in

Jerantut-Benta Road is threatened by farm encroachment and future road expansion, whereas the one along the Kota Tinggi – Mersing Road may have been destroyed by conversion of the site to an oil palm plantation.

As the number of mature seeds is usually low, ranging from only 5 to 40 per palm in each flowering episode (Dransfield 1970; pers. obs.), the long-term impact of over-harvesting of seeds for the local ornamental trade needs to be examined.

Discussion

Although many new populations were recorded, the conservation status of the genus remains threatened. Conservation measures are needed for *Johannesteijsmannia* particularly for the endangered endemics *J. magnifica, J. lanceolata* and *J. perakensis*. Key issues, challenges and suggestions pertaining to the conservation of the genus are discussed below.

Many populations of *Johannesteijsmannia altifrons* are in the lowland forests and there is a need to provide protection status to the habitats where they occur. The initiative taken by a logging licencee to conserve a portion of the *J. altifrons* population in the Temengor FR, Perak, through the High Conservation Value Forest approach should be emulated. During logging, every effort should be taken to minimise niche damage and leaving ample canopy cover.

The importance of keeping existing populations intact cannot be over-emphasised. For *Johannesteijsmannia lanceolata, J. magnifica* and *J. perakensis*, all localities should preferably be protected as they are endemics with small population sizes found in less than five localities. Several localities were found to have populations with high genetic diversity (Look 2007), i.e., Kledang-Saiong (for *J. perakensis*), Temengor (for *J. altifrons*), Kinta (for *J. magnifica)* and Sungai Lalang FRs (for *J. lanceolata*). These populations should be given utmost priority when proposals are weighted. Among these, only the populations in the Sungai Lalang FR are protected. The Sungai Lalang FR is a special area where three species, *J. altifrons, J. lanceolata* and *J. magnifica*, grow sympatrically. Regular monitoring of populations sited within several hundred metres from forest boundaries or fringes is also highly recommended because past experiences have shown that these areas are easily encroached and illegally converted into other land uses.

Palms and many understorey or herbaceous plants are traditionally ignored in forest censuses and pre-felling inventory exercises, because only some targeted economically valuable species and fruit trees are considered important. Ignorance, which eventually leads to the lack of expertise of forest managers in the field to recognise rare and threatened species, is a significant hindrance to conservation. In this respect, *Johannesteijsmannia* should be listed in the forest management plan as a species requiring conservation attention.

For some populations in logged-over forests, the after-logging effects on the demography and population viability are not documented. A long-term demographic monitoring on populations in logged-over forests, and preferably comparative studies with populations in undisturbed sites, can help to assess population health and determine further conservation actions needed to conserve the affected populations. Demographic studies have only been conducted on one undisturbed population of *J. lanceolata* in the Angsi Forest Reserve (Rozainah & Sinniah 2005, Chan 2009). The species is concentrated in valleys with densities ranging from 65 to 171 palms ha^{-1}. In a 3.2 ha plot, the ratio of seedlings, juveniles and adult was 1:3:5 (Chan 2009), indicating recruitment limitation. This could be because the population has reached the maximum carrying capacity of the environment, or failed to regenerate because of low seed production and significant seed loss. We also observed a low number of seedlings in populations of *J. perakensis* and *J. magnifica* in the respective logged-over forests of Kledang-Saiong and Berembun.

Although an export ban for all species of *Johannesteijsmannia* has been in place under the Malaysia Customs (Prohibition of Export) Order since 1998, this merely reduced demand from the international trade, but not the local trade (Chan & Saw 2009). Seeds are still being harvested indiscriminately without regulatory limits. A seed harvesting regime is needed to allow seed collection that does not jeopardise the viability and regeneration of the populations. Permits are required for seed collection and we suggest seed harvesting only at intervals of 3–5 years, during the mast flowering years when flowering and fruiting are more intense. No seed collection from a site should be allowed if the population shows poor regeneration. This can be indicated by a demography census which can be easily carried out by visual enumeration or, better still, with permanent tagging and proper count. We further recommend a certification process for plants in trade. This would encourage nurseries to establish domestication and propagation programmes and ultimately reduce harvesting pressures from the wild. Palms in cultivation are known to flower and fruit more regularly. *Ex situ* conservation should be the last resort because maintaining living collections in botanical gardens is costly and often difficult. If this option is to be adopted, priority should be given to the high-risk populations such as those on state lands.

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Appendix A. Distribution of *Johannesteijsmannia* in Malaysia. # state land; * new localities recorded since Dransfield (1972); FR – Forest Reserve.

Species	Locality	State
Johannesteijsmannia lanceolata	1. Jerantut-Benta Road #	Pahang
	2. Krau Wildlife Reserve	Pahang
	3. Angsi FR *	Negeri Sembilan
	4. Sungai Lalang FR	Selangor
Johannesteijsmannia magnifica	1. Berembun FR	Negeri Sembilan
	2. Sungai Lalang FR	Selangor
	3. Serendah FR *	Selangor
	4. Bukit Kinta FR *	Perak
Johannesteijsmannia perakensis	1. Gunung Bongsu FR *	Kedah
	2. Bintang Hijau FR	Perak
	3. Kledang Saiong FR	Perak
	4. Bubu FR	Perak
	5. Bubu FR	Perak

Johannesteijsmannia altifrons	1. Sungai Lalang FR	Selangor
	2. Temengor FR *	Perak
	3. Sungai Durian FR *	Kelantan
	4. Bukit Bauk FR *	Terengganu
	5. Bukit Bandi FR *	Terengganu
	6. G. Arong FR	Johor
	7. Jemaluang FR *	Johor
	8. Panti FR	Johor
	9. Kluang FR *	Johor
	10. Taman Negara	Pahang & Terengganu
	11. Ulu Sedili FR *	Johor
	12. Endau-Rompin State Park	Johor
	13. Kluang FR	Johor
	14. Lenggor FR	Johor
	15. Kota Tinggi – Mersing Road #	Johor
	16. Linggiu *	Johor
	17. Serasa FR	Kelantan
	18. Batu Papan *#	Kelantan
	19. Berkelah FR *	Pahang
	20. Lesong FR *	Pahang
	21. Tembat FR *	Terengganu
	22. Jerangau FR *	Terengganu
	23. Sungai Nipah FR *	Terengganu
	24. Rasau Kerteh FR *	Terengganu
	25. Pasir Raja Selatan FR *	Terengganu
	26. Bako National Park	Sarawak
	27. Kubah National Park	Sarawak
	28. Semariang Road #	Sarawak

Conservation status of *Paraboea* species (Gesneriaceae) in Malaysia

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ABSTRACT. *Paraboea* (including *Trisepalum*) is represented by 36 species in Malaysia and displays a high level of endemism (80%) and 31 of its species are restricted to limestone habitats. Two species are endemic in Sabah, of the 11 species in Sarawak 10 are endemic, and in Peninsular Malaysia 16 of the 24 species are endemic. *Paraboea culminicola* K.G.Pearce and *P. obovata* Ridl. are reinstated as distinct species and *P. madaiensis* Z.R.Xu & B.L.Burtt is reduced to synonymy in *P. sabahensis* Z.R.Xu & B.L.Burtt. Based on information from the Taxon Data Information Sheet, 15 species fall within the IUCN Category of Least Concern, four as Near Threatened, three as Vulnerable, eight as Endangered, four as Critically Endangered, and three as Data Deficient. None is Extinct. Most of the endangered species (94%) grow in Peninsular Malaysia on limestone hills that do not lie within the network of Totally Protected Areas and which are threatened by burning, quarrying and habitat destruction or disturbance, from resort development or recreation or temple activities. Assignment of conservation status is the first step in planning conservation management of endangered species, through advocating legal protection of a network of limestone hills, particularly those where critically endangered species grow (e.g., Tambun Hot Springs, Perak and the Lambok hills, Kelantan), monitoring populations of Critically Endangered species, taking steps towards resolving the status of the poorly known Data Deficient species, and the establishment of endangered species *ex situ*.

Keywords. Conservation, Gesneriaceae, Malaysia, *Paraboea*

Introduction

In Malaysia, *Paraboea* (including *Trisepalum*) is a genus predominantly of obligate limestone species with only five of the 36 species growing on other rock types, either on soils derived from quartz (*P. elegans*), sandstone (*P. obovata*), igneous rocks (*P. leopoldii*) and apparently from granite (the poorly known *P. deterigibus* and *P. paraprimulina* from Sarawak). *Trisepalum speciosum* (Ridl.) B.L.Burtt is here included because molecular work by Moeller et al. (2009) shows that it belongs in *Paraboea*.

Limestone in Malaysia is mostly of the tower karst type with a few raised coral islands in Sabah (Lim & Kiew 1997). Although limestone occupies only a very small fraction of the land area, it harbours disproportionate biodiversity, for example, in Peninsular Malaysia almost 14% of the seed plant flora grows on limestone that covers only 0.3% of the land surface (Chin 1977). There are more than 550 limestone karst hills in Malaysia, the majority being found in Peninsular Malaysia, Sabah and Sarawak have about 60 each where in Sabah most are clustered along the Sungai Kinabatangan (Lim & Kiew 1997). In Sarawak, the largest number is found in the Kuching Division and the highest karst hills in Malaysia, the massive Gunung Api and Gunung Benarat towering to 1700 m, are in the Gunung Mulu National Park (NP) (Kiew 2004). In Peninsular Malaysia, the largest number of limestone hills occur in Kelantan (about 70 are named but there are many more small outcrops), followed by Perak with about 45 named hills. Of particular importance is the limestone in Langkawi, both on the main island and about 17 islands that have been visited botanically. A few other scattered hills occur in Kedah, Pahang, Perlis, Selangor and Terengganu.

In common with other obligate limestone species, such as balsams, begonias and microchiritas, many of the species are narrow endemics that make them especially vulnerable to habitat disturbance (Kiew 1991, 2001) and the flora of these isolated limestone tower karsts are vulnerable to a variety of threats. Quarrying for cement, road metal and marble is often considered the most severe threat but, in terms of damage to the flora, the removal of the surrounding forest causes greater damage (Kiew 1997) because the vegetation of the limestone hills become vulnerable to burning associated with agricultural practices in the surrounding areas. In Sabah, secondary and logged-over forests are also prone to burning in the El Niño years (Kiew 2001). With increasing mobility, tourist and recreational activities associated with caving or rock climbing are becoming a threat and in Peninsular Malaysia construction of temples in caves and in Sabah the collecting of birds' nests from caves (Kiew 1997) all contribute to endanger the flora. Protection of the tower karst ecosystem is only assured when they fall within national or state parks or geoparks. Forest reserves offer protection provided their status does not change. However, many limestone hills are on state land and are unprotected. For these reasons, the limestone ecosystem has long been identified as one of the most endangered ecosystems in Malaysia (Davis et al. 1995a, 1995b; Saw et al. 2009; Chua et al. 2009).

The conservation status of *Paraboea* is a good indicator of the general state of conservation of the limestone flora, because its species are found on almost every limestone hill. Preliminary conservation assessments were provided in the monograph on *Paraboea* by Xu et al. (2008), who noted that the assessments would need to be revised once more accurate data were available. 'Ground truthing' is especially important in assessing the threats to the flora of limestone hills because local destructive activities have a disproportionate impact on these relatively small limestone hills and the often narrow distributions of plant species. Local knowledge largely accounts for differences between the categories assigned here compared with those of Xu et al. (2008).

Endemism and distribution

Endemism is extremely high in *Paraboea*. There are no species in common among Peninsular Malaysia, Sarawak and Sabah. The majority (23 species) of the 36

Malaysian *Paraboea* species occur in Peninsular Malaysia, with 11 species in Sarawak and two species in Sabah and within each of these areas, many species are restricted to one hill or a group of adjacent hills. Of the 23 Peninsular Malaysian species, five species extend into Peninsular Thailand that shares the same climate and topography (the political boundary cutting through a floristic zone) and two are also recorded from Sumatra (Xu et al. 2008).

Paraboea is poorly represented in Sabah. *Paraboea leopoldii* is known only from Bodgaya Island (Wong et al., 1999) while *P. sabahensis* (Fig. 3C) is more widespread. In Sarawak, paraboeas cluster in three limestone areas: Gunung Mulu NP is the most biodiverse with six species (*P. apiensis*, *P. bayengiana*, *P. candissima*, *P. clarkei*, *P. effusa* and *P. meiophylla*), two (*P. speluncarum* and *P. culminicola*, Fig. 2C) on Gunung Subis with the latter species also known from Bukit Sarang with two (*P. clarkei* and *P. havilandii*) on the many limestone hills in the Kuching Division (Kiew et al. 2004). Only *P. clarkei* (Fig. 1C) occurs on limestone in both the Kuching Division and the Gunung Mulu NP. The two non-limestone species (*P. deterigibilis* and *P. paraprimuloides*) are poorly known and are as yet each known from a single locality (See Appendix A).

In Peninsular Malaysia, the two non-limestone species are *P. obovata* that grows on sandstone in Langkawi and *P. elegans* (Fig. 2B) that grows on quartzite in Kedah, Kelantan and Selangor. The limestone species are grouped within three main phytogeographical zones. The northern floristic zone is most biodiverse with 10 species. Most are found in Langkawi and associated islands (*P. acutifolia*, *P. divaricata*, *P. ferruginea*, *P. lanata*, *P. laxa*, *P. regularis* and *P. suffruticosa*) with a few in Perlis (*P. gracillima*) or on both Langkawi and in Perlis (*P. bintangensis* and *Trisepalum speciosum*, Fig. 3B). Of these, four also occur in Peninsular Thailand.

The west coast zone (mainland Kedah, Perak and Selangor) is home to six species (*P. caerulescens* (Fig. 2A), *P. capitata* (both varieties), *P. paniculata*, *P. parviflora*, *P. verticillata* and *P. vulpina*), of which one also occurs in Sumatra. All six occur in Perak with *P. paniculata* spreading to Selangor and *P. verticillata* distributed from Selangor north to Kedah.

The central and northern zone (Kelantan, Terengganu and Pahang) is home to six species and one variety (*P. bakeri* (Fig. 1A), *P. brachycarpa* (Fig. 1B), *P. capitata* var. *oblongifolia*, *P. lambokensis* (Fig. 3A), *P. nervosissima*, *P. treubii* and *P. vulpina*), of which one species is also found in Sumatra. Only *P. capitata* var. *oblongifolia* and *P. vulpina* occur on both sides of the Main Range, i.e., in both the west coast and in the central and northern zones.

Three species, *P. gracillima*, *P. obovata* and *P. regularis* are known from a single hill and a further seven from less than five hills (*P. bakeri* (Fig. 1A), *P. bintangensis*, *P. divaricata*, *P. elegans* (Fig. 1B), *P. lambokensis* (Fig. 3A), *P. vulpina* and *P. parviflora*).

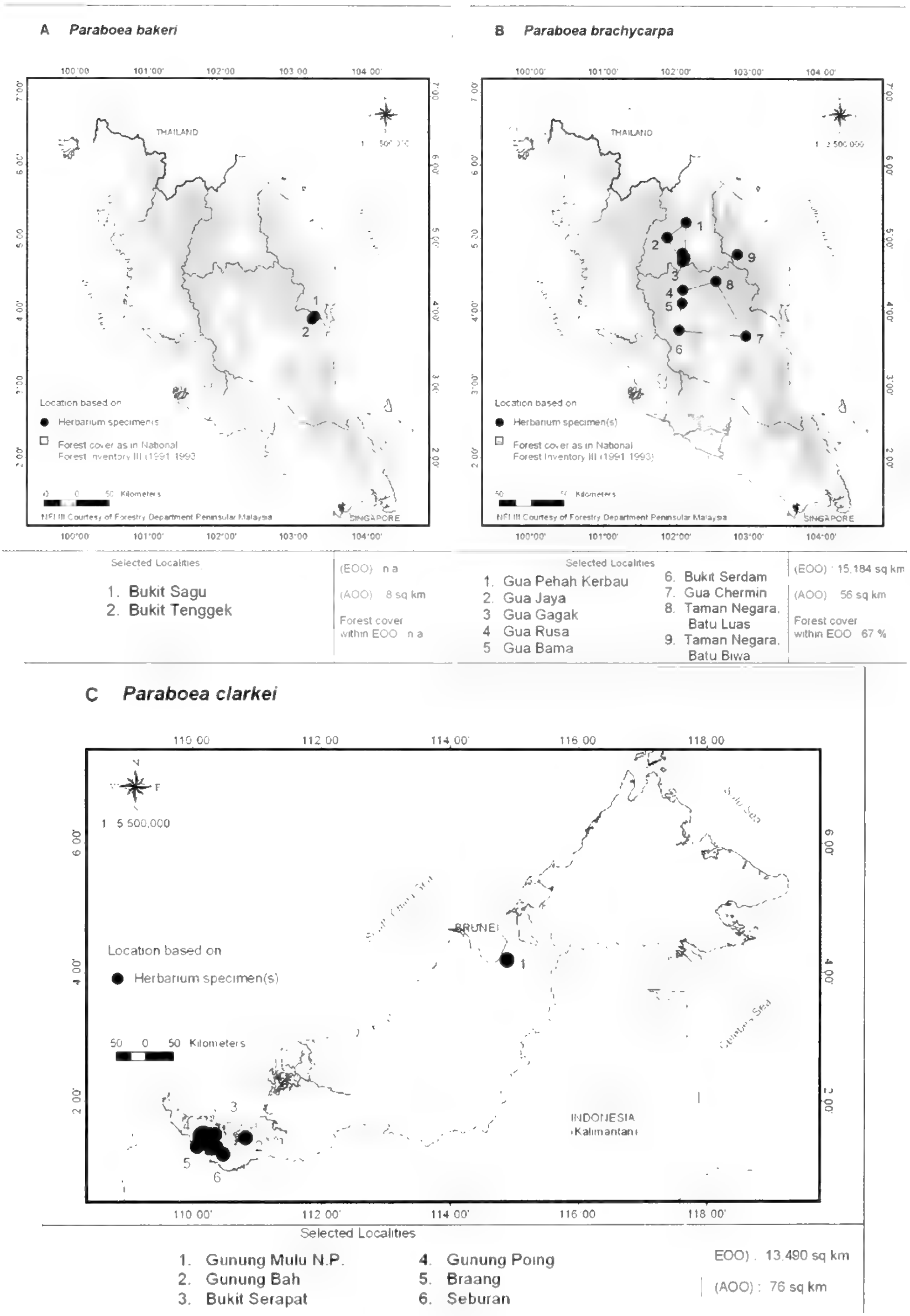


Fig. 1. Distribution of *Paraboea bakeri*, *P. brachycarpa* and *P. clarkei* in Malaysia. EOO = extent of occurrence and AOO = area of occupancy.

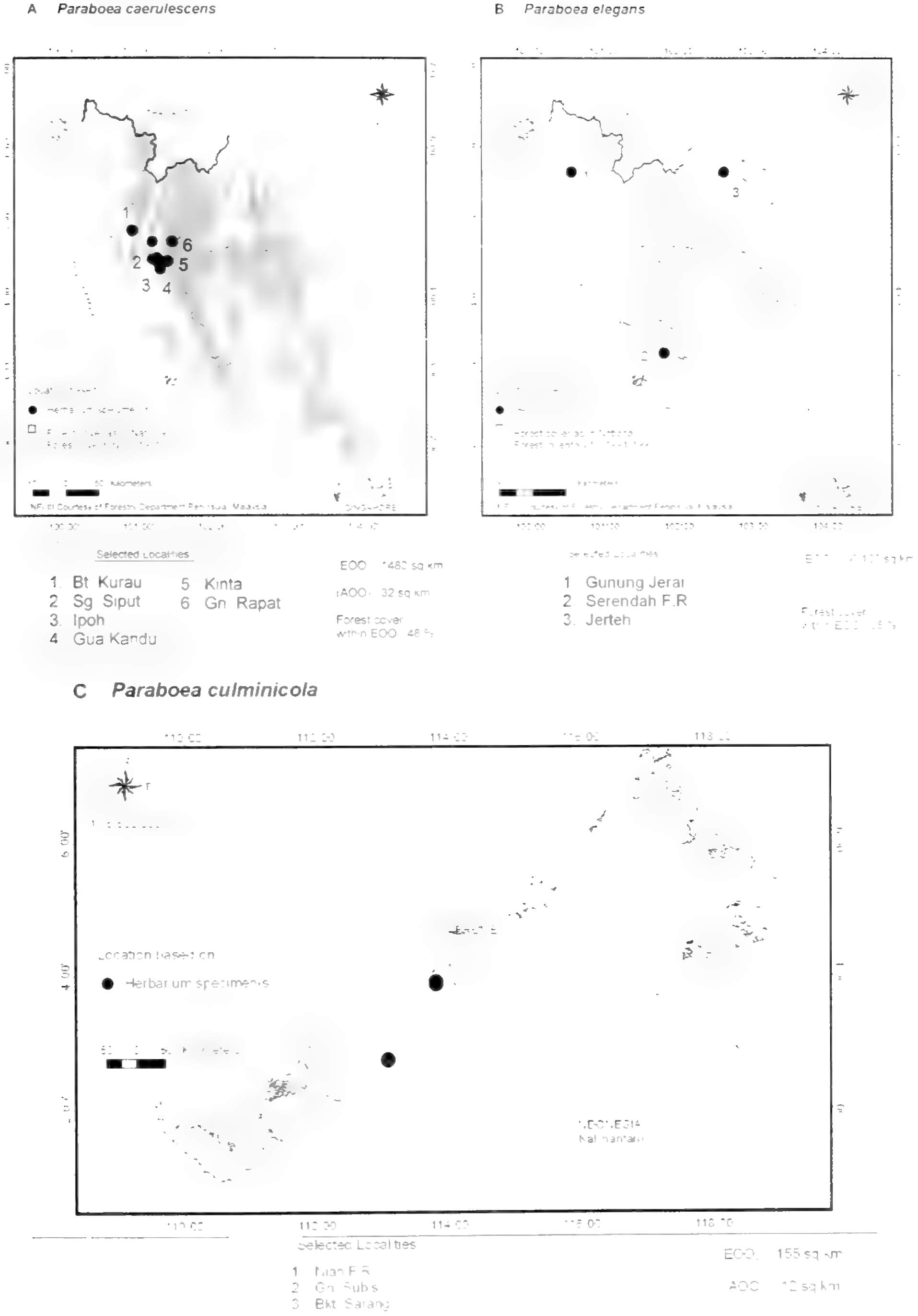
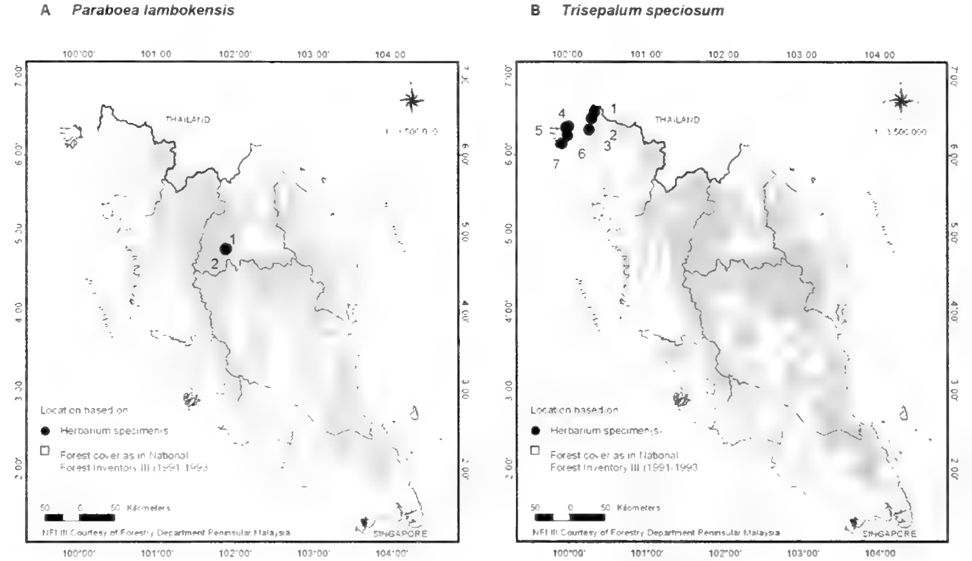
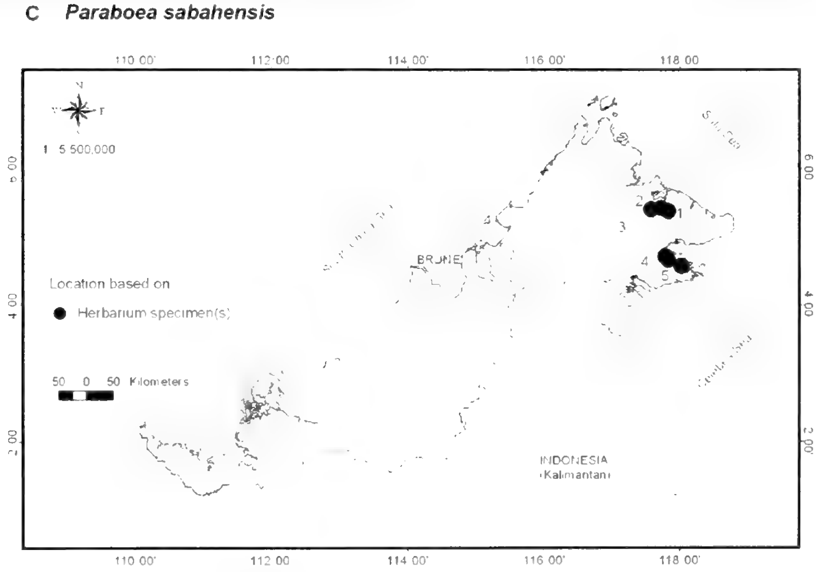


Fig. 2. Distribution of *Paraboea caerulescens*, *P. elegans* and *P. culminicola* in Malaysia. EOO = extent of occurrence and AOO = area of occupancy.



Selected Localities	
1. Bukit Senarip 2. Gua Renayang	(EOO) n a (AOO) 8 sq km Forest cover within EOO n a

Selected Localities		
1. Kaki Bukit 2. Bukit Bintang 3. Bukit Pinang	4. Pulau Anak Tikus 5. Tanjung Rhu 6. Kg Batu Puteh 7. Pulau Dayang Bunting	(EOO) n a (AOO) 28 sq km Forest cover within EOO n a



Selected Localities

1. Bilit, Sopiloring Hill 2. Gamatong 3. Bukit Batangan	4. Madai Cave 5. Bukit Tengar, Sengarong F.R.	(EOO) 2,217 sq km (AOO) 32 sq km

Fig. 3. Distribution of *Paraboea lambokensis*, *Trisepalum speciosum* and *Paraboea sabahensis* in Malaysia. EOO = extent of occurrence and AOO = area of occupancy.

Conservation status

To assess the conservation status of each taxon, the Taxon Data Information Sheet (TDIS) is completed to provide the baseline data for the assessment (Chua & Saw 2006). This includes taxonomic information, habitat and distribution, mapping of the extent of occurrence (EOO) and area of occupancy (AOO), legal protection status, threats and population decline, current conservation measures, utilisation, and finally the Red List category and criteria based on the IUCN Red List Categories & Criteria, Version 3.1, 2001 (hppt://www.iucn.org/) including the arguments for listing. For these *Paraboea* species, data are based on the literature, herbarium specimens and field work over a 30-year period. The information in the TDIS is then discussed with one of the national assessors before it is accepted. The conservation status applies to the situation in Malaysia, i.e., it is a regional conservation status except for endemic species, where it becomes the global status.

The most commonly used criteria are geographic distribution, limited number of populations, protection status and population decline. For the last criterion, ground truthing is essential. In a few cases an entire hill has been given over for quarrying, e.g., Gunung Pondok (Perak) and Bukit Sagu (Pahang), are currently being quarried and eventually will be razed to the ground. In most cases, only part of a hill is affected by quarrying. In other cases, where the hills are on stateland, burning associated with agricultural practices poses the major threat. This affects *Paraboea* species differently depending on their niche requirements.

There are basically two groups of paraboeas in Malaysia, the ones with erect stems, whorled decurrent leaves that are often covered in silvery indumentum, and have purple flowers and twisted fruits; compared with the other group that are rosette plants, with opposite petiolate leaves, white or pinkish flowers and straight fruits. The former group grows in full sun on sheer vertical rock faces above the tree canopy or on jagged summits. They are relatively resilient to disturbance because they may be positioned above the burning of the surrounding vegetation and because their seeds can invade bare rockfaces. In addition, they often occur in large numbers. The latter group, in contrast, in most cases (*P. laxa* is an exception) are species that grow at the base of the hill below the tree canopy on damp shaded rocks or rock faces, where they are found as small local populations. These species are particularly vulnerable to all types of disturbance. Because paraboeas occupy these different microhabitats, it is common to find two species occurring on the same hill, for example, in the Kuching limestone *P. havilandii* grows exposed on the summits and *P. clarkei* in damp shaded habitats below the canopy.

No Malaysian species is extinct but 40% (VU, EN and CR species) are endangered, with most (93%) of these occurring in Peninsular Malaysia (Table 1). This is because most of the limestone areas in Sarawak (Gunung Mulu and Niah NPs) are totally protected. In contrast in Peninsular Malaysia, the great majority fall outside protected areas, namely the Langkawi World Heritage Geopark, Perlis State Park, or on the six limestone hills in Taman Negara (Gunung Peningat, Batu Luas, Batu Subis, Gua Telingga, Batu Biwa and Batu Ta'at), so that only eight species are

Table 1. Conservation status of Malaysian taxa of *Paraboea* following IUCN Categories & Criteria, ver. 3.1 (2001).

	Number of taxa		
Category	*Peninsular Malaysia*	*Sarawak*	*Sabah*
Extinct (EX)	0	0	0
Critically Endangered (CR)	4	0	0
Endangered (EN)	7	0	1
Vulnerable	3	0	0
Near Threatened (NT)	3	1	0
Least Concern (LC)	6	8	1
Data Deficient (DD)	1	2	0

totally protected. In addition, in Peninsular Malaysia relatively few hills fall within Permanent Reserved Forests.

Species that require conservation action are those that fall within the CR and DD categories. The three DD species (*P. deterigibilis*, *P. paraprimuloides* and *P. regularis*) are all poorly known species, known from single specimens, some with doubtful taxonomic standing (see Appendix A). Efforts need to be made to obtain better material before their conservation status can be assessed.

Four species, all from Peninsular Malaysia, fall within the CR category. All, *P. bakeri* (Fig. 1A), *P. lambokensis* (Fig. 3A), *P. parviflora* and *P. vulpina*, are known from three or fewer localities where they have small populations that grow on the damp shaded base of a hill or in mossy damp crevices or on hills that are particularly vulnerable to disturbance. All the hills where they are found are on state land. The most critically endangered is without doubt *P. bakeri* because the only two hills from where it is known are both actively being quarried. For these CR species, a three-pronged approach needs to be taken. The first is to monitor the populations to ensure that further population decline does not occur, the second is to inform the relevant stakeholders of their existence and to enlist their support in protecting the areas from further disturbance, and thirdly to collect seed or leaf material for *ex situ* collections. Already a plant-rescue project to grow and propagate *P. bakeri ex situ* has started.

Conservation of the limestone flora

The totally protected areas in Sarawak and in Langkawi and Taman Negara, Peninsular Malaysia, offer protection to about half the species of *Paraboea*. Conservation of paraboeas highlights the situation facing the limestone flora in general because, in common with groups of plants that are restricted to limestone habitats, most species are not widespread but have restricted distributions and lie within a particular floristic zone and a few are confined to one or a few hills. Therefore, a network of hills, as is the case in Sarawak, needs to be legally protected because with the high biodiversity of the limestone flora, no single hill conserves more than a fraction of the flora. There is now sufficient data to identify hills that either harbour narrow endemics or are particularly rich in endangered species.

In protecting these tower karsts, it is important that a buffer zone of forested vegetation surrounds them to protect against accidental burning as a result of agricultural practices. This is crucial in preserving the damp, shaded habitat that many paraboeas (and other limestone species) need. In addition, regular monitoring of critically endangered species is necessary to prevent population decline.

In Malaysia, the limestone flora has repeatedly been recognised as one of the critically endangered habitat types (Davis et al. 1995a, 1995b; Kiew 1994; Saw et al. 2009; Chua et al. 2009) and has been identified as one of the Important Plant Areas (IPAs). One of the targets in the Malaysian National Strategy for Plant Conservation is to conserve 50% of the IPAs (Saw et al. 2009). For example, Chua et al. (2009) have already suggested that the limestone hills in the Meropoh Gua Musang area of Kelantan be included within Taman Negara. This would conserve at least one population of CR species, *P. vulpina*, as well as *P. nervosissima*.

Mapping distribution patterns and assigning conservation status is the first step in identifying endangered species and biodiversity hotspots that will enable a holistic programme to be formulated that can balance the protection and conservation of the limestone ecosystem with the various commercial, recreational and religious uses. This is particularly critical in Perak where as yet no hill is protected and where many hills are actively being quarried or the flora is being degraded by resort or recreational development or activities associated with temples. Mapping shows that the most important hill in Perak from the point of view of conservation of *Paraboea* species is the Tambun Hot Springs (sometimes called Ayer Hangat), which is home to two CR species *P. parviflora* and *P. vulpina*, as well as the Perak endemic *P. capitata* var. *capitata*. Mapping also pinpoints those species that are known from a single or very few hill(s), such as *P. lambokensis* from Gua Renayang and Gua Senarip, Kelantan.

This study on the conservation status of *Paraboea*, being based on sound taxonomy and recent field surveys, serves as a model for the study of other groups of plants that are either obligate limestone species or are endemic to Peninsular Malaysia, Sabah and Sarawak. It aims at producing a map to show the distribution of endangered species and those hills that require gazetting as Totally Protected Areas.

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Appendix A. Conservation status of *Paraboea* and *Trisepalum* species (Gesneriaceae) in Malaysia.

1. ***Paraboea acutifolia*** (Ridl.) B.L.Burtt
Distribution: Peninsular Malaysia and S Thailand
Habitat: On limestone rocks in forest
Conservation status: LC in Malaysia
Notes: Some populations lie within the Langkawi World Heritage Geopark. Xu et al. (2008) note that it is considered threatened in Thailand.

2. ***Paraboea apiensis*** Z.R.Xu
Distribution: Endemic in Sarawak (Gunung Api)
Habitat: On limestone rocks.
Conservation status: LC
Notes: Gunung Api lies within the Gunung Mulu National Park.

3. ***Paraboea bakeri*** M.R.Hend. (Fig. 1A)
Distribution: Endemic in Peninsular Malaysia (Bukit Sagu, Pahang)
Habitat: Small populations on moss cushions in high shaded crevices in limestone hills where water seeps down
Threats: Bukit Sagu and the adjacent small Bukit Tenggek are in the process of being totally destroyed by quarrying.
Conservation status: CR B2b(iii) + c(iv)
Notes: Xu et al. (2008) gave this species a conservation status of EN B1ab(ii, iii, iv) based on one collection from a second locality, Gua Charas. However, this species has not been recollected from this hill suggesting that this specimen is wrongly localised. In 2011, both these hills were surveyed and the small population of plants discovered was collected for *ex situ* propagation in the Forest Research Institute Malaysia Nursery. Eventually this species will certainly become extinct in the wild.

4. ***Paraboea bayengiana*** B.L.Burtt
Distribution: Endemic in Sarawak (Gunung Mulu and Gunung Benarat)
Habitat: On limestone rocks
Conservation status: LC
Notes: All its populations fall within the Gunung Mulu National Park.

5. *Paraboea bintangensis* B.L.Burtt
Distribution: Endemic in Peninsular Malaysia (Langkawi, Perlis)
Habitat: On limestone rockfaces in light shade
Threats: Its three localities fall outside totally protected areas.
Conservation status: EN B1ab(iii)
Notes: Xu et al. (2008) gave this species a conservation status of VU D2.

6. *Paraboea brachycarpa* (Ridl.) B.L.Burtt (Fig. 1B)
Distribution: Endemic in Peninsular Malaysia (Kelantan, Pahang and Trengganu)
Habitat: On summits and exposed limestone cliff faces, where it occurs in sizeable populations.
Conservation status: LC
Notes: Known from many hills, including two within Taman Negara.

7. *Paraboea caerulescens* (Ridl.) B.L.Burtt (Fig. 2A)
Distribution: Endemic in Peninsular Malaysia (Perak)
Habitat: On summits and exposed vertical limestone rock faces
Threats: It is recorded from 6 hills, none of which fall within the network of Totally Protected Areas and many are actively being quarried or house temples or are on state land that is disturbed by development and/or agriculture.
Conservation status: EN B2ab(iii)
Notes: The Batu Kurau locality is part of the Gunung Pondok massif that is currently being razed to the ground for cement. Xu et al. (2008) gave this species a conservation status of LC on the assumption that it is known from 'several sites over a wide area and there are no major threats'. The specimen from Pahang (Gua Charas) listed in Xu et al. (2008) is based on a misidentification.

8. *Paraboea candidissima* B.L.Burtt
Distribution: Endemic in Sarawak (Gunung Buda and Gunung Benarat)
Habitat: On limestone rocks
Conservation status: LC
Notes: All localities lie within the Gunung Mulu National Park.

9a. *Paraboea capitata* Ridl. **var. *capitata***
Distribution: Endemic in Peninsular Malaysia (Perak).
Habitat: Near base of limestone hills, on damp shaded rocks faces and in gullies
Threats: Although it is recorded from about 5 hills, none falls within the network of Totally Protected Areas and many are actively being quarried or house temples or are on state land that is disturbed by development and/or agriculture.
Conservation status: EN B2ab(iii)
Notes: The type specimen of *P. capitata* (together with the type specimens of its synonyms *P. curtisii* Ridl. and *P. polita* Ridl.) were all collected by Curtis on 28th December 1895 from Gunung Bujang Melaka, Perak. However, this is a granite mountain and apart from these collections *P. capitata* has never been collected on anything other than limestone and, although Gunung Bujang Melaka has been visited by other botanists on several occasions, this species has not been recollected from there. Prior to visiting Gunung Bujang Melaka on the way from Ipoh to Kuala Dipang, Curtis had 'examined the limestone hills at three or four places' (Curtis 1896) so it is probable that a mistake was made in labelling these specimens.

9b. *Paraboea capitata* Ridl. **var. *oblongifolia*** Ridl.

Distribution: Endemic in Peninsular Malaysia (Perak and Kelantan)

Habitat: Near base of limestone hills, on damp shaded rocks faces and in gullies

Threats: Although it is recorded from two states and from about four hills, none falls within the network of Totally Protected Areas and many are actively being quarried or house temples or are on state land that is disturbed by agriculture and/or development.

Conservation status: EN B2ab(iii)

Notes: The two varieties are distinct in the lamina size and shape. Collections from limestone labelled Bukit Kurau and Padang Rengas both refer to different parts of the Gunung Pondok massif that is currently being razed to the ground for cement.

10. *Paraboea clarkei* B.L.Burtt (Fig. 1C)

Distribution: Endemic in Sarawak (Kuching Division and Gunung Mulu National Park)

Habitat: On shaded limestone rocks below the tree canopy, common where it occurs.

Conservation status: LC

Notes: It is protected within the G. Mulu National Park. It is the only species in Sarawak to be collected from more than one phytogeographical area. The Mulu population has much larger leaves (24–26.5 × 11.5–12 cm) as compared with the Kuching Division specimens (11.5–16 × 6–8.5) and perhaps deserves to be recognised as a distinct variety.

11. *Paraboea culminicola* K.G.Pearce (Fig. 2C)

Distribution: Endemic in Sarawak (Gunung Subis, Bukit Sarang)

Habitat: On summits and exposed vertical limestone cliffs

Conservation status: NT

Notes: It is protected within the Niah National Park. Xu et al. (2008) considered this species synonymous with *P. treubii*. *Paraboea culminicola* is clearly different in its oblanceolate leaves in whorls of 4 with 35–40 pairs of veins and cinnamon-brown undersides, and in its inflorescences with large floral leaves and the peduncles of the side branches that are c. 8 times longer that the ultimate branches. So it is here treated as a distinct species.

12. *Paraboea detergibilis* (C.B.Clarke) B.L.Burtt

Distribution: Billiton, Bangka and W Sumatra, Indonesia, and Sarawak (Gunung Gaharu).

Habitat: Not known but Gunung Gaharu, Kuching Division, is not a limestone mountain.

Conservation status: DD in Malaysia

Notes: Xu et al. (2008) reported this species in Sarawak from a single specimen. The population on Gunung Gaharu needs to be relocated before the status of this species can be assessed.

13. *Paraboea divaricata* (Ridl.) B.L.Burtt

Distribution: Endemic in Peninsular Malaysia (Langkawi).

Habitat: On limestone rocks

Threats: Known from 2 or 3 localities, it nowhere occurs within a Totally Protected Area.

Conservation status: EN B2ab(iii)

Notes: Xu et al. (2008) gave this species a conservation status of VU D2 on the grounds that the Ayer Hangat site falls within a Forest Reserve.

14. *Paraboea effusa* B.L.Burtt
Distribution: Endemic in Sarawak (Gunung Mulu National Park)
Habitat: On limestone rocks in forest and also on the summit of limestone karsts.
Conservation status: LC
Notes: Fully protected within the Gunung Mulu National Park.

15. *Paraboea elegans* (Ridl.) B.L.Burtt (Fig. 2B)
Distribution: Peninsular Malaysia (Kedah, Kelantan and Selangor) and S Thailand.
Habitat: In light shade on quartzite outcrops, on Gunung Jerai, Kedah, at 1000 m and in Kelantan and Selangor at c. 300 m.
Threats: The rocky habitats where it grows are vulnerable to disturbance, for example, on Gunung Jerai by tourist pressure, at the Kelantan site by maintenance work to the nearby hydroelectric dam and in Selangor by logging that has caused landslips at the base of the outcrop.
Conservation status: VU B2ab(iii) in Malaysia
Notes: Xu et al. (2008) included *P. obovata* as a synonym of this species but it is quite different (see 25. *P. obovata* below).

16. *Paraboea ferruginea* (Ridl.) Ridl.
Distribution: Endemic in Peninsular Malaysia (Langkawi)
Habitat: On limestone rocks in damp, shaded places
Conservation status: NT
Notes: Known from several sites on the main and smaller islands of Langkawi, some of which lie within the Langkawi World Heritage Geopark.

17. *Paraboea gracillima* Kiew
Distribution: Peninsular Malaysia and S Thailand
Habitat: It occurs in small populations on shaded limestone cliffs from the base under forest canopy to near the summit
Conservation status: LC in Malaysia
Notes: It grows within the Perlis State Park.

18. *Paraboea havilandii* (Ridl.) B.L.Burtt
Distribution: Endemic in Sarawak (Kuching Division)
Habitat: On the summit and on exposed limestone cliffs where it is quite common
Conservation status: LC
Notes: This species is common and collected from many hills. The specimen cited by Xu et al. (2008) from Pahang (*Henderson SFN 25250*) is in fact the type specimen of *Emarhendia bettiana* (M.R.Hend.) Kiew et al.

19. *Paraboea lambokensis* Kiew (Fig. 3A)
Distribution: Endemic in Peninsular Malaysia (Kelantan)
Habitat: Small populations grow at the base of limestone cliffs or around cave mouths in light shade
Threats: The two hills (Gua Senarip, Gua Renayang) are on state land surrounded by agriculture that has removed the surrounding forest cover leaving the population vulnerable to burning.
Conservation status: CR B1b(iii) + c(iv)

20. *Paraboea lanata* (Ridl.) B.L.Burtt
Distribution: Endemic in Peninsular Malaysia (Langkawi).
Habitat: On limestone rocks by the seashore or in rocky hillsides on limestone islands.
Conservation status: VU B2ab(iii)
Notes: Known from several localities on Langkawi and several minor islands, some of which fall within the Langkawi World Heritage Geopark.

21. *Paraboea laxa* Ridl.
Distribution: Endemic in Peninsular Malaysia (Langkawi).
Habitat: On limestone rock faces and summits
Conservation status: VU B1ab(iii)
Notes: Known from several localities on Langkawi and several minor islands, some of which fall within the Langkawi World Heritage Geopark.

22. *Paraboea leopoldii* K.M.Wong, J.T.Pereira, Sugau & S.P.Lim
Distribution: Endemic in Sabah (Bodgaya Island)
Habitat: Its localised populations grow on exposed igneous rocks from 4 m above the shoreline to high up on vertical cliffs.
Threats: Its population is difficult to access since it grows on rocky headlands and along the coast.
Conservation status: LC
Notes: Xu et al. (2008) erroneously recorded this species from limestone.

23. *Paraboea meiophylla* B.L.Burtt
Distribution: Endemic in Sarawak (Gunung Benarat)
Habitat: On limestone rocks
Conservation status: LC
Notes: Totally protected within the Gunung Mulu National Park.

24. *Paraboea nervosissima* Z.R.Xu & B.L.Burtt
Distribution: Endemic in Peninsular Malaysia (Kelantan, Pahang)
Habitat: Exposed summit and vertical limestone cliffs
Conservation status: LC
Notes: Quite widespread with some localities lying within Taman Negara.

25. *Paraboea obovata* Ridl.
Distribution: Endemic in Peninsular Malaysia (Langkawi).
Habitat: In heath forest, in light shade on sandstone rocks.
Conservation status: LC
Notes: This species is known only from Gunung Machinchang, a sandstone hill that lies within the Langkawi World Heritage Geopark. *Paraboea obovata* has been considered as a synonym of *P. elegans* (Burtt 1984, Xu et al. 2008), perhaps because both species do not grow on limestone. However, they are clearly different. *Paraboea obovata* has opposite, obovate leaves that measure 6–7.5 × 2.2–4 cm and has a distinct petiole 1.2–4.5 cm long and peduncles 9–11 cm long. In contrast, *P. elegans* has whorled, narrowly lanceolate leaves 4 × 1.7 cm and either lacks a petiole or has a short petiole c. 1 cm long, and it has long peduncles 15–18.5 cm long. For these reasons, *P. obovata* is therefore here reinstated as a distinct species.

26. *Paraboea paniculata* (Ridl.) B.L.Burtt

Distribution: Peninsular Malaysia (Perak, Selangor) and Sumatra.

Habitat: On the summit and vertical limestone cliffs

Threats: None of the hills where it is found lies within the network of Totally Protected Areas. Only Bukit Takun lies within a Forest Reserve but vegetation of this hill is disturbed by the activities of rock climbers.

Conservation status: EN B2ab(iii) in Malaysia

Notes: Xu et al. (2008) gave this species a conservation status of LC because it 'has been collected at several sites over a wide area and there are no major threats'.

27. *Paraboea paraprimuloides* Z.R.Xu

Distribution: Endemic in Sarawak (Hose Mountains)

Habitat: Growing on cliffs, but not on limestone

Threats: Unknown.

Conservation status: DD

Notes: This species is known only from the type collection made in 1967 and is still incompletely known. Until the population has been relocated, its conservation status cannot be assessed. Xu et al. (2008) gave this species a conservation status of CR B1ab(ii,iii,v) on the presumption that species known only from the type are confined to the area where they were collected and that their extent of occurrence is below 100 km^2.

28. *Paraboea parviflora* (Ridl.) B.L.Burtt

Distribution: Endemic in Peninsular Malaysia (Perak)

Habitat: Very uncommon and where it occurs it is found in small populations in shaded gullies in limestone cliffs below the tree canopy.

Threats: None of the four limestone hills where it occurs lies within the network of Totally Protected Areas and all are no longer surrounded by forest but are heavily disturbed by tourism (Gunung Tempurung), resort development (Ayer Hangat as the Tambun Hot Springs is sometimes known) or quarrying (Kinta).

Conservation status: CR B2ab(iii)

Notes: Xu et al. (2008) gave this species a conservation status of LC stating that 'the relatively few collections ... are almost all from protected areas and there are no major threats'.

29. *Paraboea regularis* (Ridl.) Ridl.

Distribution: Endemic in Peninsular Malaysia (Langkawi) and S Thailand.

Habitat: Not known

Conservation status: DD in Malaysia

Notes: For Peninsular Malaysia, it is known only from the type specimen which comprises detached leaves and inflorescences taken from a plant grown in the Singapore Botanic Gardens in 1893. In spite of Langkawi being well-collected, this species has not re-found, which raises the possibility that it is a Thai species.

30. *Paraboea sabahensis* Z.R.Xu & B.L.Burtt, Edinb. J. Bot. 48 (1991) 12. Type: Sabah, Kinabatang District, Bilit, Sopiloring Hill, *Ampuria SAN 35269* 18 April 1963 (holo E; iso K, L, SAN, SAR). (Fig. 3C)

Synonym nova: Paraboea madaiensis Z.R.Xu & B.L.Burtt, Edinb. J. Bot. 48 (1991) 4. Type: Sabah, Semporna District, Madai Caves. *Tamura & Hotta 722* (holo E; iso KYO).

Distribution: Endemic in Sabah (Kinabatangan and Semporna Districts)
Habitat: On exposed summits and vertical limestone hills, quite common locally
Threats: Batu Tengah Cave, Bilit, and Bukit Batangan limestone hills lie within very disturbed forest or secondary forest that in Sabah is prone to burning in El Niño years, while the limestone vegetation is somewhat disturbed on Gunung Madai and Bukit Dulong Lambu (Gomantong) because they are the most important caves in Sabah for the collecting of bird nests. However, a summit species can withstand some disturbance, for example, the population on Bukit Dulong Lambu has spread onto summit areas laid bare by the Great Burn in 1982/83.
Conservation status: EN B2ab(iii)
Notes: With the collection of specimens from more populations, it has become clear that the differences in lamina shape and size, including shape of the leaf base, and petiole length that were used to distinguish between *P. sabahensis* and *P. madaiensis* are not discrete. *Paraboea sabahensis* is preferred for the name of this species because of its wider distribution with the consequence that *P. madaiensis* is reduced to synonymy.

31. *Paraboea speluncarum* (B.L.Burtt) B.L.Burtt
Distribution: Endemic in Sarawak (Gunung Subis).
Habitat: On limestone growing in light shade on stalactites from the arch of cave mouths.
Conservation status: LC
Notes: It lies within the Niah National Park.

32. *Paraboea suffruticosa* (Ridl.) B.L.Burtt
Distribution: Endemic in Peninsular Malaysia (Langkawi).
Habitat: On limestone karsts
Conservation status: NT
Notes: It is known from several localities on the main island and from smaller islands, some of which lie within the Langkawi World Heritage Geopark.

33. *Paraboea treubii* (H.O.Forbes) B.L.Burtt var. *treubii*
Distribution: Peninsular Malaysia (Kelantan, Pahang) and Sumatra.
Habitat: Not common, it grows exposed on summits and on vertical limestone cliffs.
Conservation status: LC in Malaysia
Notes: Some of the hills on which it occurs lie within Taman Negara.

34. *Paraboea verticillata* (Ridl.) B.L.Burtt
Distribution: Endemic in Peninsular Malaysia (Kedah, Perak, Selangor)
Habitat: Common, growing exposed on summits and vertical limestone cliffs
Threats: None of the hills where it is found lie within the network of Totally Protected Areas. Only Bukit Takun lies within a Forest Reserve but vegetation of this hill is disturbed by the activities of rock climbers.
Conservation status: EN B2ab(iii)
Notes: Xu et al. (2008) gave this species a conservation status of LC because it "has been collected at several sites over a wide area and there are no major threats".

35. ***Paraboea vulpina*** Ridl.

Distribution: Peninsular Malaysia (Kelantan, Perak) and S Thailand.

Habitat: Small, local populations on the shaded base of vertical limestone cliff faces.

Threats: None of the three hills from where it is known is protected within the network of Totally Protected Areas or is surrounded by forest. All are in heavily disturbed areas close to agriculture or tourist developments.

Conservation status: CR B2ab(iii) in Malaysia

Notes: Xu et al. (2008) gave this species a conservation status of LC because 'although this species is only known from a few collections it is found over a large area and several of the known sites are in protected areas and there are no major threats'.

36. ***Trisepalum speciosum*** (Ridl.) B.L.Burtt (Fig. 3B)

Distribution: Peninsular Malaysia (Langkawi, Perlis) and S Thailand.

Habitat: On exposed summits of limestone hills

Conservation status: NT in Malaysia

Notes: It is known from several localities on the main island of Langkawi and from smaller islands, some of which lie within the Langkawi World Heritage Geopark. It also grows on the mainland.

Utricularia (Lentibulariaceae) habitat diversity in Peninsular Malaysia and its implications for conservation

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ABSTRACT. *Utricularia* is a cosmopolitan carnivorous genus with more than 30 species in Malesia, of which 14 occur in Peninsular Malaysia. *Utricularia* species exhibit a range of habits including free-floating or affixed aquatic, semi-aquatic, terrestrial, lithophytic or epiphytic. In terms of habitat preference, three arbitrary groups are recognised, namely, habitat specialists, habitat generalists, and open and wayside pioneers. This grouping allows information on niches to be interpreted into conservation management measures. One third of the Peninsular Malaysian species are habitat specialists, found either in single localities or in one microhabitat. Among them, *U. furcellata* and *U. scandens* are listed as 'Critically Endangered' for the Red List for Peninsular Malaysia, whereas *U. involvens* and *U. punctata* are 'Vulnerable' and *U. vitellina* is 'Rare'. Four species, *U. caerulea, U. gibba, U. striatula* and *U. uliginosa*, are found in many sites and microhabitats and are thus considered generalists, with their conservation status varying from 'Vulnerable' to 'Least Concern'. *Utricularia aurea, U. bifida* and *U. minutissima* are adaptable pioneers able to co-exist with weeds and they may also be indicators of past disturbance. Two rare species, *U. limosa* and *U. subulata*, have not been relocated recently and their local habitat preferences are uncertain.

Keywords. Conservation, habitat diversity, Peninsular Malaysia, *Utricularia*

Introduction

Utricularia L. (Lentibulariaceae) is a large genus of carnivorous plants, with c. 220 species worldwide and c. 30 species in Malesia (Taylor 1989). It is cosmopolitan, found in all continents from subarctic landscapes to tropical rain forest, at oases in deserts and on oceanic islands (Brummit 2007). To date, 14 species are recorded from Peninsular Malaysia.

The genus has a unique body plan among flowering plants as highlighted by Rutishauser & Isler (2001). *Utricularia* has no true root; the rudimentary anchoring rhizoids lack a root cap. Its stolons have randomly arranged phloem and xylem instead of the collateral vascular bundles typical of angiosperm stems. The foliar organs or leaves arise at the bases of peduncles or along stolons. Leaf laminas of the terrestrial species are often minute, while in the aquatic species they are much dissected. The inflorescences are racemes with indefinite growth, sometimes branched or twining. The minute traps are highly modified, glandular organs arising from the leaves, stolons or rarely from other parts. These traps function to supplement their nutrient intake by trapping microfauna, microflora and microbes (Richards 2001, Sirova et al. 2009). In Peninsular Malaysia, *Utricularia* is found almost exclusively in nutrient-poor environments with low pH.

Three species of *Utricularia* in Peninsular Malaysia are free-floating aquatics from the section *Utricularia*, that includes *U. aurea* Lour., *U. gibba* L. and *U. punctata* Wall. ex A.DC., of which the latter two also exist as affixed aquatics. Nine species are terrestrials that are sometimes semi-aquatic. They are *U. minutissima* Vahl from section *Meionula*, *U. caerulea* L. from section *Nigrescentes*, *U. limosa* R.Br. from section *Nelipus*, *U. subulata* L. from section *Setiscapella* and *U. bifida* L., *U. involvens* Ridl., *U. scandens* Benj., *U. uliginosa* Vahl and *U. vitellina* Ridl. from section *Oligocista*. There are only two species of minute and rosette lithophytic herbs, namely *U. furcellata* Oliv. and *U. striatula* Sm. from section *Phyllaria*, which at times are terrestrial or epiphytic within the cloud forest or waterfall splash zones.

Authors prior to Ridley gave little mention of the ecology and distribution of *Utricularia* species found in the region. Ridley (1893, 1895, 1901, 1908, 1923), Henderson (1928) and Spare (1941) provided background knowledge on the habitats and commonness of local *Utricularia* but held slightly different opinions on taxonomic delimitation. Taylor's (1977) treatment of the genus in Malesia detailed the distribution and ecology for every taxon, although this was not specific to Peninsular Malaysia. Turner (1995) summarised habitat information provided by Ridley and Taylor in his plant checklist for the Peninsula but did not add new information. Parnell's (2005) account on Thai *Utricularia* provided ecological details on habitat and substrate type, altitudinal range and flowering period, of which eleven of the Peninsular Thailand species also extend into Peninsular Malaysia.

This study was carried out as part of the revision of *Utricularia* for the Flora of Peninsular Malaysia. It aimed to document the range of habitats and niches occupied by various *Utricularia* species, to understand the implications of their distribution ranges and habitat preferences, and to formulate conservation measures based on the assessments of such information. For non-endemic species, the Red List status obtained is only applicable to Peninsular Malaysia.

Materials and methods

General collection was carried out at various wet habitats to obtain materials of the common and widespread species, and specialised fieldtrips were organised to relocate rare species at specific sites. Habitat information including GPS readings, elevation, exposure, substrate type, water depth, pH, associated plants, range of niches occupied and known history of disturbance were recorded for specimens collected in the field. Relevant label information for existing herbarium specimens was databased. In the absence of any habitat records, information was inferred from the Kepong BRAHMS gazetteer database.

Table 1. Criteria for arbitrary habitat-preference groupings.

Habitat-preference group	Number of collection localities	Microhabitat specificity	Tolerance to disturbance
Habitat specialists	1–2	≤ 5 niche subtypes	Pristine / lightly disturbed (by trails etc.)
Habitat generalists	> 3 (≤ 25)	> 5 niche subtypes	Mostly in or near natural vegetations
Open / wayside pioneers	Many (≥ 30)	> 8 niche subtypes	Mostly disturbed (abandoned land)

The lowest and highest spatial range occupied by a species was shown by the elevation data. Latitude and longitude of collection sites were plotted with ArcView to generate the Extent of Occurrence (EOO) and Area of Occupancy (AOO) maps. Three arbitrary habitat-preference groups were established according to criteria listed in Table 1.

Conservation assessment was carried out following the IUCN Red List Categories and Criteria version 3.1 (2001). The assessment was largely specimen based; verified or published records were included when specimen information was lacking. The Taxon Data Information Sheets (TDIS) modified from the IUCN Red List Assessment Questionnaire to suit the requirements for local plants, as recommended by the Malaysia Plant Red List guidebook (Chua & Saw 2006), were then completed for each species. TDIS comprises five parts, i.e., Taxon Attributes, Geographical Range and Demographic Details on Population, Red List Category and Criteria Assessment, Current Conservation Measures for the Taxon and Utilisation.

Habitat preferences and the associated population size data provided the basis for the IUCN Red List criterion A, scoring on population reduction. EOO, AOO and distribution patterns were used to evaluate the Criterion B, scoring on geographical range, which has been designed to identify populations with restricted, declining or fluctuating distributions in the present or near future (IUCN 2010).

Results and discussion

Microhabitat types, biotic and abiotic properties and altitudinal range

In Peninsular Malaysia, *Utricularia* occurs in a range of perpetually or seasonally wet microhabitats—from pristine lowland and montane swamps to fairly disturbed, meso-eutrophic ditches, as detailed in Appendix A. The aquatics usually occupy the open shallow waters; the terrestrials or semi-aquatics grow on multifarious waterlogged or shallowly inundated soils; lithophytic species often grow on rock-faces with dripping water. Some of these habitats are subject to periodic drought, where the annual or ephemeral *Utricularia* populations die out in the dry months. In line with the cost-benefit model for carnivorous plants (Givnish et al. 1984), the genus generally prefers sunny, moist and low-nutrient habitats with low pH (3–7). Some species are able to tolerate deep shade and eutrophic waters but do not flower under such conditions.

The altitudinal range of the genus extends from the coastal *Typha* reed beds in Pulau Langkawi to the montane sandstone plateau of Gunung Tahan, the highest peak in Peninsular Malaysia at 2187 m. Edaphic conditions and light availability are more crucial in determining the presence or absence of *Utricularia*, rather than altitude. It is not found in mangroves, coastal lagoons, inland salt-licks and hot springs, due to its intolerance for high pH and salinity; nor reservoirs with steeply shelving shores, large swift rivers and concrete waterways which do not provide stable substrate for establishment. The genus is generally absent from tall-forested areas with closed canopies while being fairly common along streams, heaths, swamps, along forest fringes, in forest gaps, trails or other edaphic and biotic vegetation types nestled within the climactic forests, wherever there is adequate sunlight and moisture.

Habitat preferences and conservation status

The habitat specialists are species that are found only in a single locality or one type of microhabitat. One third of species from the Peninsula falls within this group. The habitat generalists consist of plants that are found in many sites and suited to live in many types of wet microhabitat but rarely found in heavily disturbed sites. Common pioneers of open and wet-habitat are adaptable plants that are able to co-exist with weeds and may indicate past disturbance.

The conservation status of a particular species is related to its habitat-preference because this affects its overall distribution and commonness. If the particular locality where a species is found is within a protected area, the conservation status then falls into a much lower category, as listed in Table 2. However, although population decline is perceived as minimal in protected areas for most plants, the type of fringe habitats *Utricularia* favours is often sacrificed in the process of amenity or trail development, or depleted by high-impact or uncontrolled recreational activities. Thus, their survival is not fully guaranteed, especially for the habitat specialist and habitat generalist.

Habitat specialists

Utricularia furcellata (Fig. 1A) is a new record for Peninsular Malaysia (Chew et al. 2011). It is differentiated from the more common *U. striatula* as detailed in Appendix B and Fig. 2A–B. *Utricularia furcellata* grows in a localised population on the montane heath of Gunung Ayam, within Gunung Stong State Park, Kelantan. The species is previously known to grow on moist rocks (1500–2700 m) in North-eastern India and mossy wet tree boles and rocks in lower montane forest (>1700 m) in Northern Thailand. In Kelantan, *U. furcellata* exists as a terrestrial herb on a patch of white-sandy heath within the cloud forest zone inundated with a thin film of water. The site is traversed by a major hiking trail. Up to 2003, the trail was reported to receive an average of more than 2500 climbers (out of 5000 visitors to the area) annually with an increasing trend (Maseri et al. 2006).

Table 2. Conservation status of *Utricularia* species in Peninsular Malaysia in relation to habitat preferences. CR = Critically Endangered; VU = Vulnerable; RA = Rare; NT = Near Threatened; LC = Least Concern; DD = Data Deficient.

Habitat preference	Species	Conservation status	Rationale used in assessment
Habitat specialist	*U. furcellata*	CR	Single microhabitat in State Park but with heavy trekker traffic
	U. scandens	CR	Single microhabitat in State Park with natural catastrophe (flash flood) risk
	U. involvens	VU	Single protected locality but affected by amenity development
	U. punctata	VU	Last remaining protected locality with invasive waterweed risk
	U. vitellina	RA	Sensitive montane species in 2 protected localities
Habitat generalist	*U. caerulea*	VU	Highland pink form in 2 protected localities; lowland white form experiencing population decreased
	U. striatula	NT	Fairly common in mountainous waterways but sensitive to drought
	U. uliginosa	NT	Fairly common in acidic swamps but always within forested areas
	U. gibba	LC	Fairly common in acidic open waters
Open / wayside pioneer	*U. aurea*	LC	Most common aquatic *Utricularia* in Peninsular Malaysia
	U. bifida	LC	Common pioneer in wayside nutrient-poor wet habitats
	U. minutissima	LC	Fairly common in natural and wayside nutrient-poor wet habitats
Uncertain	*U. subulata*	DD	Last collected in 1925, not rediscovered, sites developed
	U. limosa	DD	Single collection in 1937, site developed

Utricularia scandens (Fig. 1B) used to be recorded from a number of rocky heaths or ridges that were constantly inundated on the small isolated hill range of the Gunung Ledang State Park, Johor (Ridley 1901). Gunung Ledang is popular among local and foreign tourists and received more than 11,000 visitors annually (Suksuwan & Ong 2005). According to the description by Ridley and nature guides who trekked the hill since the 1980s (Gan & Kueh, pers. comm.), the rocky heaths originally had

Fig. 1. Habit and habitat of four *Utricularia* species. **A.** *Utricularia furcellata* from the Gunung Ayam heath, Gunung Stong State Park. **B.** *Utricularia scandens* at Padang Batu, Gunung Mering, Gunung Ledang State Park. **C.** *Utricularia involvens* at Gunung Jerai Forest Reserve, Kedah. **D.** *Utricularia punctata* at the Tasik Bera RAMSAR site, Pahang.

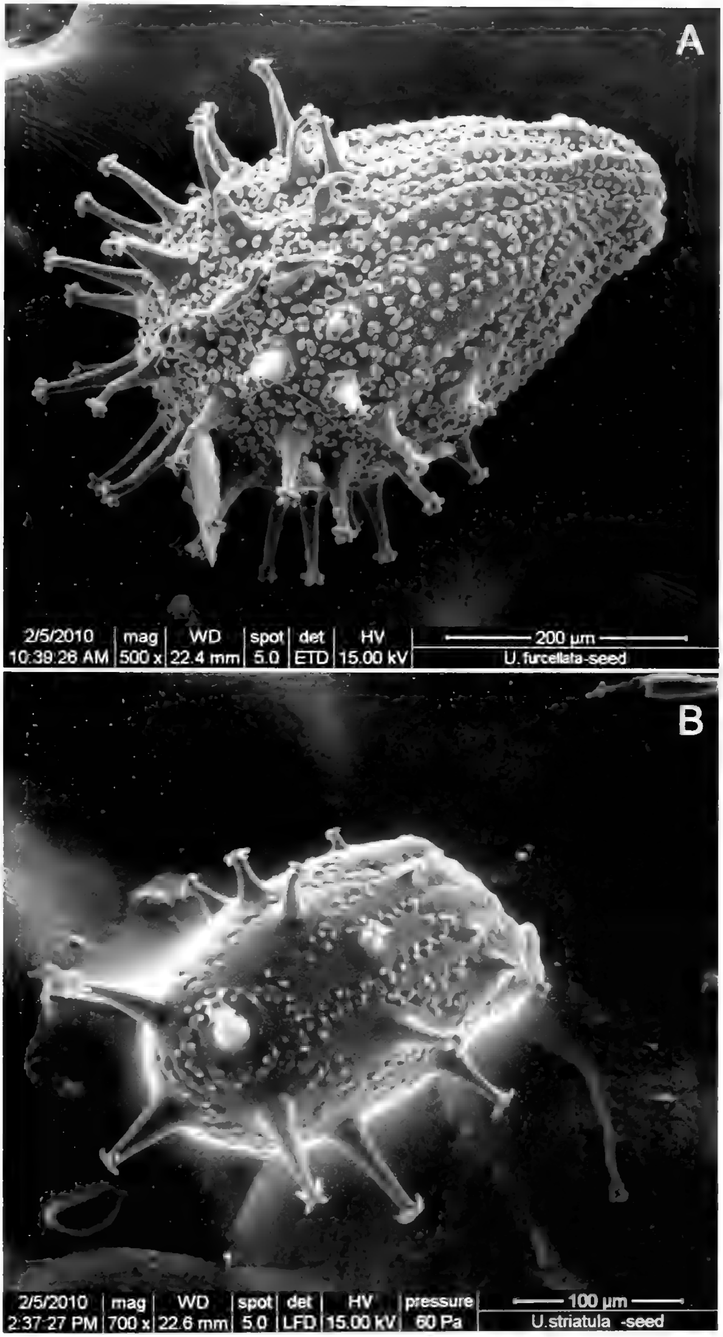

Fig. 2. Scanning electron microscopy images of *Utricularia* seeds. **A.** *Utricularia furcellata* seed showing periclinal testa cell-walls densely covered with globose or shortly clavate verrucae and the long processes that end in knobbly, clavate tips; size c. 455 µm. **B.** *Utricularia striatula* seed showing relatively smooth periclinal testa cell-walls with verrucae occurring only along sinuate boundaries, and short processes with glochidiate, stellate tips, size c. 251 µm.

sparse forested cover on thin soils and were constantly inundated by a thin film of seepage that flowed from the peaty, wooded ridges higher up. Much of the tracks along the rocky heath and the narrow summit ridge lost part of their vegetation cover either from the firewood cutting, campsite clearing or trees toppling over on heavily trampled soils, exposing the bedrock. Further soil erosion and loss of ground cover followed in these areas, which eventually caused the microhabitats to dry up. Parts of the trails and campsites along the waterways were littered and polluted by human waste that resulted in siltation and algal blooms in slow-flowing or stagnant waters. By the time the State Park was established in 1997 under the Johor National Parks Cooperation and stricter rules were enforced against destructive camping practices, *U. scandens* populations were depleted from all previously known collecting spots that were impacted by heavy tourist traffic. It was recently relocated from Padang Batu on Gunung Mering, a remote rocky heath above the Lampung Jatuh waterfall. The particular site was later destroyed by a rare flash flood event, further reducing the population.

Both *U. furcellata* and *U. scandens* are found in single microhabitats at one restricted site, making them highly susceptible to localised disturbance and microclimate changes. The case of *U. scandens* is a typical instance in which a sensitive species occupying an open microhabitat fringing a waterway frequented by human trekkers would inevitably disappear from the intensively utilised zones, persisting only in the more inaccessible sites. The current management practices in the two State Parks do not restrict current or future use of the sites where these sensitive species occur, hence qualifying both species 'Critically Endangered' status.

Although occurring in a variety of microhabitats, *U. involvens* (Fig. 1C) has never been found outside the Gunung Jerai Forest Reserve, Kedah. There it occurs in various open to shaded wet microhabitats. Although protected, the site is a popular tourist spot with an army camp at the summit. The species is under much pressure from amenity development and this has already led to some previously wet sites drying out. Being susceptible to local microclimate change, the conservation status of this species is scored as 'Vulnerable'.

Utricularia punctata (Fig. 1D) grows in slow-flowing, shallow open water. Habitat conversion affecting the backwaters of Sungai Pahang and Kota Tinggi, and the introduction of the noxious weed from South America, *Cabomba furcata* Schult. & Schult.f. in Roem. & Schult., that had taken over the niche of *U. punctata* in Tasik Chini, has probably wiped out the original population of the species in these places. Currently, it is surviving in Tasik Bera, Pahang—the largest freshwater lake in Peninsular Malaysia that is protected as a RAMSAR wetland site. Although locally abundant, it warrants a 'Vulnerable' status from the risk of being displaced by invasive aquatic weeds.

The sole endemic species for Peninsular Malaysia, *U. vitellina*, is found only on the two highest summits in Peninsular Malaysia, on montane peaty bryophyte mounds usually along stream banks. The highest peak, Gunung Tahan, is located within Taman Negara Pahang, while Gunung Korbu, Perak, lies within a forest reserve. Although locally abundant in the two protected sites, this species occurs only in one type of microhabitat and is currently absent from the campsites and most parts along the trails. It is susceptible to disturbance from human activities and microclimate change, and is given a 'Rare' status.

Wet habitat generalists

Utricularia caerulea has two flower colour forms in Peninsular Malaysia. White-flowered populations are mostly lowland terrestrial plants, found in wet, sandy or muddy sites. Only two collections of plants with white flowers have been made after 1980, the others were collected from 1890 to 1964. The pink-flowered form is a terrestrial or semi-aquatic plant that grows along stream banks, and has only been recorded from Gunung Jerai and Gunung Ledang. Although the species was previously found in many sites and occupies a variety of habitats, the white-flowered form of the lowlands is becoming rare while the pink-flowered form is restricted to two sites. It is therefore given a 'Vulnerable' status.

Found on major mountain peaks and a few large waterfalls, *U. striatula* is either a minute terrestrial, lithophytic or is an epiphytic herb. *Utricularia uliginosa* is usually found in the lowlands and sometimes in the highlands. It is a stout terrestrial or semi-aquatic *Utricularia* of peat swamps, heaths and forest edges. Despite being found in many sites and able to adapt to many different microhabitats, these two 'Near Threatened' species appear to be sensitive to human disturbance and are not found outside naturally vegetated areas.

Another *Utricularia* that is rarely found away from natural habitats is *U. gibba*. The species grows in slow-flowing to stagnant waters usually bordering dryland forest or peat swamps. It sometimes colonises old man-made water bodies but has never been seen in an eutrophic lake. This species is thus given a 'Least Concern' status.

Wet habitat pioneers

Utricularia bifida and *U. minutissima* are two common terrestrial or semi-aquatic species found in open wayside wetlands and grasslands. Naturally, both are restricted to open stream banks or heath but have managed to colonise many man-made areas with fairly established vegetation and relatively stabilised soil and are often found in association with each other.

Utricularia aurea is the most common aquatic free-floating *Utricularia* found locally, usually in slow-flowing or stagnant water. Although commonly found in ditches around agriculture areas, it is not known to be weedy. Like all other *Utricularia* species, it is sensitive to all forms of fertiliser, and is noticeably absent from intensively worked paddy fields and eutrophicated old mining lakes, although it had been reported as common in these habitats by Ridley (1923) and Spare (1941).

Rare species with uncertain habitat preferences

Utricularia limosa was last recorded from low-altitude swamps in 1925 by Holttum, while *U. subulata* was last collected from Teluk Merbau, Selangor, in 1937. Repeated attempts to relocate these species from previously known sites has yielded nothing.

All the historical collection sites have been converted to built-up areas, agricultural or degraded lands. Due to a lack of information, both species are given a 'Data Deficient' status. Both species are possibly already exterminated in Peninsula Malaysia. However, because the plants of these species are so minute they could still be extant but overlooked in other wet habitats. Existing records are not specific in regard to habitat preferences and could not be verified on-site recently, leaving them with uncertain habitat preferences.

Conclusion

Utricularia is a carnivorous plant genus that grows in various wet habitats subjected to seasonal water fluxes. From field observations and growth experiments, the species are generally sensitive to changes in water nutrient content, pH, humidity, the micro-organism community and microclimate. Therefore, where they might occur, *Utricularia* species (especially those that fall within the habitat specialist group) could serve as convenient indicator species for quick assessments of the health of a habitat. The balance between habitat generalists and common pioneer species can help indicate the level of disturbance or recovery of a habitat. Conservation monitoring efforts can therefore be broadened from the species to the habitat perspective.

The initiatives of the state and federal governments of Peninsular Malaysia in setting up and managing the respective parks and reserves deserve commendation. In order to maximise the species conservation role of these protected areas while allowing recreational use, the current management practices could be further refined to cater for naturally occurring fringe species. As it stands, zonation is mostly pre-determined by accessibility or remoteness. Strict conservation zones should be re-aligned to capture different microhabitat types instead of conveniently using rivers and ridges as boundaries and assigning all the open-vegetated microhabitats as campsites. Periodic closure, especially in the wet seasons, is pivotal in preventing irreversible transformation of inundated sites and erosion in steep areas. Continuous documentation of the local flora is also essential in providing baseline information so that any degradation to the plant community that is associated with substandard amenity development or overuse can be pin-pointed.

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Appendix A. Habitat information on *Utricularia* species in Peninsular Malaysia. Notes: *No details available from specimens; information adopted from [1]Taylor (1989), [2] Ridley (1923).

Species	Altitude (m)	Substrate [water pH]	Habitat notes
Section *Meionula*			
U. minutissima	0–2100	Wet, damp or rarely dry mud, silt, sand, laterite and shallow soil overlying rocks [4–6(–7.5)]	Exposed damp ground in lowlands and highlands; peat swamp edges; lowland heaths; highland sphagnum bog; rockfaces of waterfalls or rapids; lowland river or stream banks; lowland and highland mammal trails; wayside turfs and fields; roadside seepages; constructed wetlands; recorded previously in rice fields and old mining areas
Section *Nigrescentes*			
U. caerulea	0–1400	Damp or wet sand, laterite, silt and shallow soil overlying rocks [4.5–6 (–7)]	Lowland and highland heaths; highland stream banks; swamps; recorded previously in wet grasslands
Section *Oligocista*			
U. bifida	0–1100	Wet, damp or rarely dry mud, silt, sand, laterite and shallow soil overlying rocks [4–6(–7.5)]	Exposed damp ground in lowlands and highlands; peat swamp edges; lowland heaths; lowland river or stream banks; lowland mammal trails; wayside turfs and fields; roadside seepages; constructed wetlands; recorded previously in rice fields

U. involvens	700–1200	Damp or wet mud and shallow soil overlying rocks [3.5–6]	Highland exposed to shaded stream banks; highland exposed to shaded wet rockfaces; wet grasslands; exposed to shaded springs and wells; wet montane road-cut outcrops
U. scandens	300–1000	Damp or wet sand, mud and shallow soil overlying rocks [c. 5(–6)]	Highland heath or wet grasslands on rocky heaths
U. uliginosa	0–1000	Seasonally flooded, damp or wet mud, peat and sand [(3–) 3.5– 6.5 (–7)]	Exposed to shaded forest edges; highland and lowland rocky stream banks; peat swamps; highland sphagnum bog; highland mammal trails; shallow pools; exposed to shaded springs and wells
U. vitellina	1500–2100	Damp or wet bryophyte peat mound [3.5–5]	Exposed to shaded montane mossy banks
Section *Phyllaria*			
U. furcellata	c. 1500	Gently sloping, damp (white) sand and mud [c. 5]	Exposed heaths nestled within lower montane forest
U. striatula	150–2100	Damp, wet or dripping rock and tree trunk [3.5– 5.5]	Highland exposed to shaded, mossy earth banks; highland exposed to shaded wet rock faces; waterfall or rapid splash zones; tree trunks or branches within splash zones; wet montane road-cut outcrops
Section *Setiscapella*			
*U. subulata**	coastal plain	Wet or damp sand and shallow soil overlying rocks[1] [n.a.]	Low open marshes; ditches; stream and pool sides[1]
Section *Nelipus*			
*U. limosa**	coastal plain	Wet sand and mud[1] [n.a.]	Open country wet spots[2]; swamps; pool margins; lowland shallow waters[2]
Section *Utricularia*			

U. aurea	0–1300	Often edges of still or slow flowing water, rarely wet or damp mud and silt [3–7(–7.5)]	Peat swamp edges; river backwaters; open wetlands; puddles in open fields; *gelam* swamp forests; tidal *typha* reed beds; natural or man-made lakes, ponds, reservoirs, dams and depressions; old oil palm estate, village or wayside ditches and canals; abandoned rice-field patches or organic rice-fields; ex-mining ponds; constructed wetlands; recorded previously in highland catchment pond
U. gibba	0–1300	Often shallow and sometimes deep, still or slow flowing water with low pH, sometimes wet or damp mud and silt [3–5.5(–7)]	Peat swamp edges; river backwaters; open wetlands; tidal *typha* reed beds; natural or man-made lakes and ponds; ditches and canals bordering peat swamps or forests; abandoned rice-field patches or organic rice-fields; constructed wetlands; tanks; recorded previously in highland catchment pond
U. punctata	0–250	Often edges of still or slow flowing black water with low pH, rarely wet or damp mud and silt [3–5]	Various niches at the edge of natural lakes; recorded previously in river backwaters

Appendix B. Taxonomic notes on the *Utricularia furcellata* specimen of Peninsular Malaysia. Vegetatively, *Utricularia furcellata* is very similar to *U. striatula* from the same section *Phyllaria*. They can be differentiated by the following micromorphological details.

	U. furcellata	*U. striatula*
Lower corolla lip	More-or-less 4-lobed, lateral lobes much smaller than the apical pair	More-or-less regularly 5-lobed
Average seed length	455 µm (N = 15)	251 µm (N = 15)
Periclinal testa cell-walls	Densely covered with globose or shortly clavate verrucae	Relatively smooth with verrucae only along the sinuate boundaries
Papillae	Densely papillate, processes long with knobbly, clavate tips	Sparsely papillate, processes short with glochidiate, stellate tips

Note: the lower corolla lip of the Kelantan specimen (*Chew et al.* FRI53603) is only shallowly lobed compared to the plants recently recorded from Northern Thailand (Suksathan & Parnell 2010), but the flower and inflorescence dimensions and descriptions match that of Taylor (1989).

Establishment of Enrekang Botanic Garden, South Sulawesi: an effort to conserve plant diversity in the Wallacea region

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ABSTRACT. The Enrekang Botanic Garden is newly established in Kabupaten Enrekang, South Sulawesi, Indonesia, to document and conserve the diversity of plants from the Wallacea Region. The new botanic garden is a collaborative venture since 2005, in which Kebun Raya Bogor is assisting the local authorities of Sulawesi Selatan to form a development plan and establish the garden's living collections. The garden has developed nursery facilities, an irrigation system, and road access. A total of 4601 living plants have been planted, representing 36 families, 156 genera and 232 species.

Keywords. Enrekang Botanic Garden, Indonesia, plant diversity, Sulawesi, Wallacea

Establishment of new botanic gardens in Indonesia

The establishment of new botanic gardens in Indonesia is in line with Article 9 of the Convention on Biological Diversity, on *Ex Situ* Conservation (CBD 1993): "establish and maintain facilities for *ex situ* conservation of and research on plants, animals and micro-organism, preferably in the country of origin of genetic resources"; and Target 8 of the Global Strategy for Plant Conservation (GSPC 2002): "sixty per cent of threatened plant species in accessible *ex situ* collections preferably in the country of origin, and ten per cent of them included in recovery and restoration programmes".

Indonesia has committed to international conventions such as the CBD (1993), Agenda 21 in 1992 (United Nations 2009) and GSPC (2002), and as part of this commitment has been establishing new botanic gardens as *ex situ* conservation sites. This activity was also included in Agenda 21 Indonesia (United Nations Development Programme & Indonesia Kantor Menteri Negara Lingkungan Hidup 1997). The establishment of new botanic gardens in every province in Indonesia will benefit not only the local community, but also represent national and international needs; for example, the conservation of plant species, soil and water by a botanic garden will not only benefit the local community but also a much wider area (Sutrisno 2010). A botanic garden also serves to inspire a wider community to respect plants and their wise use.

The establishment of new botanic gardens in Indonesia was initiated by the then Indonesian President, Megawati Sukarno Putri, during "Hari Kebangkitan

Teknologi Nasional" (the National Technology Awareness Day) on 11 August 2004, when she emphasised the importance of establishing a botanic garden in every province in Indonesia. The Minister of Research and Technology followed up on the President's speech by issuing a letter to all Governors in Indonesia (Surat Edaran Menteri Riset dan Teknologi kepada seluruh Gubernur di Indonesia No. 77/M/VIII/2004). The Minister suggested the Governors establish at least one botanic garden in each province, and to collaborate with the Indonesian Institute of Sciences (LIPI) to undertake the task. As a result, many proposals were sent to LIPI to establish botanic gardens. Consequently, from 2004 until the end of 2009, 16 Local Authorities had started to establish new botanic gardens. One of them is Enrekang (Fig. 1).

Fig. 1. Location of new botanic gardens (white circles) and the four long-established botanic gardens of Kebun Raya Indonesia (black squares) in Indonesia. (After Sutrisno 2010)

Wallacea

The Wallacea region is one of the world's biodiversity hotspots situated east of the Wallace line—an imaginary line dividing Indonesia into two floral regions: an Asian floristic region to the west and an Australian floristic region to the east. Wallacea is somewhat transitional between the two flora regions, and contains floristic elements from both regions. The area covers the islands of Sulawesi, Lombok, Lesser Sunda (including Timor Leste) and the Moluccas (see Fig. 2).

Wallacea has a high extent of floral and faunal endemism, although in general, information on the flora from the region is still lacking. However, it is estimated that c. 10,000 species of vascular plant grow in the region, of which 1500 species (15%) are endemic (Conservation International 2007).

Sulawesi is the largest island in the region, covering about 53% of the area, with c. 500 endemic species of plants. Although many new species have been discovered from the island since several decades past, the island's plant diversity is still poorly known as the number of specimens collected per 100 km^2 is still quite low, i.e., 23, whereas, ideally, an adequate representative of collections would be 100

Fig. 2. The Wallacea region: a transition zone from Australia to Asia.

specimens per 100 km^2 (Whitten et al. 2002). Moreover, this plant diversity needs to be represented in *ex situ* living collections in botanic gardens.

Sulawesi's plant diversity is facing serious threats, as also happens in the region generally, due to habitat loss, deforestation, plantation development and farming. The establishment of a new botanic in Kabupaten Enrekang, South Sulawesi, is therefore timely. The new garden is named Kebun Raya Enrekang.

Establishment of Kebun Raya Enrekang

In August-September 2005, the Local Auhorities of Enrekang in collaboration with Kebun Raya Bogor (KRB) and The National Survey and Mapping Coordination Agency (Bakosurtanal) surveyed and mapped some prospective localities as potential sites for the new Kebun Raya Enrekang (KRE). Following the survey, an MoU was signed by LIPI and the Enrekang Local Authorty for the establishment of KRE. At the same time, a master plan of the new garden was completed (PT. Tata Guna Patria 2006). In April 2006 a team from KRB worked together with some local staff to clear the site and started a nursery. A year later, some of the plant collections were officially planted in the garden on 14 March 2007 by VIPs from both Enrekang and LIPI. This first planting is regarded as the establishment date of the new garden.

KRE is located on the main Trans Sulawesi road between Makassar and Tana Toraja. It is situated at the Batu Mila Village, Kecamatan Meiwa, Kabupaten

Enrekang, Province of Sulawesi Selatan (3°33'47.58"S 119°45'40.56"E). Covering 300 ha in area with an elevation range of 70–155 m asl, the new garden is administered by the local authority Dinas Kehutanan dan Perkebunan. Since the development of KRE in 2006, the number of plant collections (excluding the nursery's collection and orchids) is 4601 accessions, comprising 36 families, 156 genera and 232 species; some of which are listed in Table 1. The new garden has 18 employees, six of whom have attended a training course on managing botanic gardens at the Kebun Raya Bogor. There is a building that functions as a temporary management office as well as a short-term accommodation for employees, a 3-km road access, nursery facilities including awning and shading, and an irrigation system, fencing around the garden that also keeps free-ranging cattle out, a motorbike, and two gazebos built by teams from KRB.

Table 1. Some plants already established in the KRE living collections.

Plant name	Family
Aleurites moluccana (L.) Willd.	Euphorbiaceae
Borassus flabellifer L.	Arecaceae
Cinnamomum celebicum Miq.	Lauraceae
Cyrtostachys microcarpa Burret	Arecaceae
Diospyros blancoi A.DC.	Ebenaceae
Diospyros celebica Bakh.	Ebenaceae
Eucalyptus deglupta Blume	Myrtaceae
Mimusops elengi L.	Sapotaceae
Myristica lancifolia Poir.	Myristicaceae
Neonauclea celebica Merr.	Rubiaceae
Pangium edule Reinw.	Achariaceae
Parkia timoriana Merr.	Fabaceae
Pigafetta elata (Mart.) H.Wendl.	Arecaceae
Pterospermum celebicum Miq.	Malvaceae
Sandoricum borneense Miq.	Meliaceae
Sapindus rarak DC.	Sapindaceae
Schleichera oleosa (Lour.) Oken	Sapindaceae
Syzygium malaccense (L.) Merr. & L.M.Perry	Myrtaceae
Syzygium zeylanicum (L.) DC.	Myrtaceae
Timonius stipulosus Valeton	Rubiaceae
Vatica pauciflora Blume	Dipterocarpaceae
Vitex cofassus Reinw. ex Blume	Lamiaceae

KRE focuses on collecting plant species native to Wallacea. Some examples include the palms *Pigafetta* and *Borassus flabelliber*, the tree genus *Agathis*, the gum tree *Eucalyptus deglupta*, the rosewood *Pterocarpus indicus* and the fragrant sandalwood *Santalum album*. The collecting sites have so far included the forests surrounding Enrekang to start with. Also, seeds have been brought from Kebun Raya Bogor.

There are some themed displays and other features to be built at KRE (see Master Plan in Fig. 3), namely, Taman Wangi (aromatic plant collections), Formal Garden, Amphitheatre, Landscaped Corridor, Herb Garden, Aquatic Plant Collections, Taman Mexico (succulent collections), Orchidarium, Pandan Garden, Palm Garden and Flower Park.

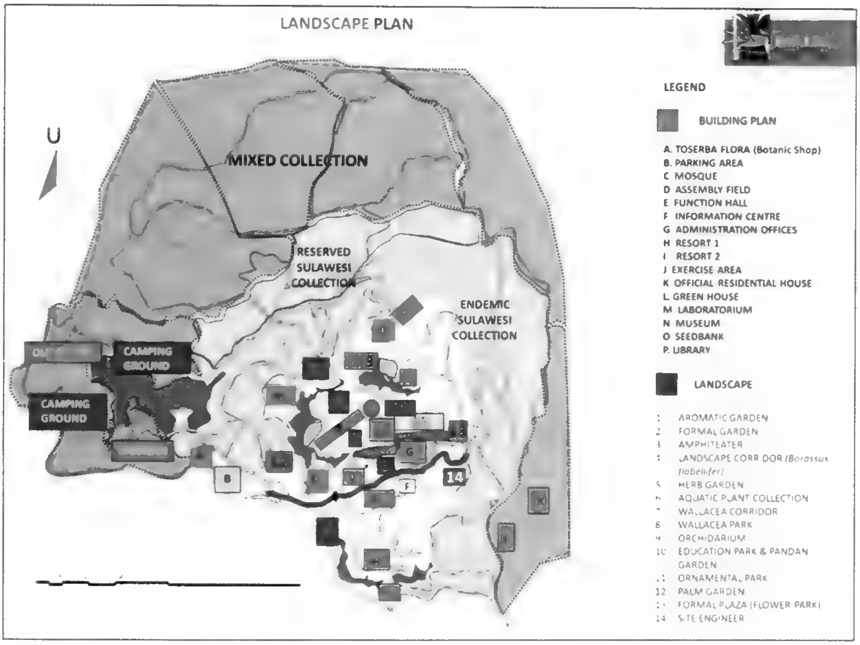

Fig. 3. Landscape plan of Kebun Raya Enrekang (taken from the Master Plan of Kebun Raya Enrekang, PT. Tata Guna Patria 2006).

Closing remarks

Establishment of a new botanic garden in each province of the vast Indonesian Archipelago is crucial as forests become more degraded and pressures to natural habitats increase due to the country's high population. The establishment of Kebun Raya Enrekang plays an important role in the conservation of plant diversity, particularly in Wallacea.

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Comparative pollen morphology of three *Alternanthera* species (Amaranthaceae)

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ABSTRACT. The pollen morphology of three *Alternanthera* species, *A. sessilis* (L.) R.Br. ex DC., *A. bettzickiana* (Regel) G.Nicholson and *A. paronychioides* A.St.-Hil., is reported. Pollen grains of *Alternanthera* are dodecahedric, isopolar and small (12.56–23.57μm). The pollen morphology of the green and red varieties of *A. sessilis* shows no significant difference in the polar length [t (98) = -1.35, $p > 0.05$] and equatorial diameter [t (98) = 1.32, $p > 0.05$]. Apertures of *A. sessilis* and *A. bettzickiana* are pantoporate with twelve round pores, whereas the pollen grains of *A. paronychioides* distinctly differ from the other two species in having eighteen oval pores. The pores of all the species are covered by rectangular, sinuous, or elongated ektexinous bodies. The sexine is metareticulate and tectum perforate with unevenly distributed perforations at the top and base of the mesoporia, except in the pollen grains of *A. bettzickiana*, in which the perforations are distributed unevenly at the top of the mesoporia only.

Keywords. *Alternanthera*, Amaranthaceae, pollen morphology

Introduction

Alternanthera Forssk. (Amaranthaceae) consists of 80 species distributed in the tropics and subtropics (Mabberley 2008). Of these, palynological data of 20 species have been reported (Table 1). The majority of these species originated from the New World (Borsch 1998, Eliasson 1988, Müller & Borsch 2005b, Nowicke & Skvarla 1979), India (Kajale 1940, Mittre 1962, Rao & Shukla 1975), Pakistan (Bashir & Khan 2003, Perveen & Qaiser 2002) and China (Li et al. 1993, Liang et al. 1978). Therefore, it would be interesting to study the pollen morphology of the *Alternanthera* species in Malesia particularly in Peninsular Malaysia, and compare these observations with the earlier data.

This is especially meaningful as in recent years, detailed study of pollen morphology has helped to resolve the relationship among members of the Amaranthaceae (Borsch 1998, Müller & Borsch 2005b). Palynological data has also supported the findings in phylogenetic studies of the subfamily Gomphrenoideae (Sánchez del-Pino et al. 2009, Müller & Borsch 2005a).

Though Erdtman (1966) has reported that the pollen grains of *Alternanthera* species possess deeply recessed pores, the apertures are not well studied. The pollen morphology of *Alternanthera* is further defined by Borsch (1998) and described as the

Table 1. References to published palynological studies on *Alternanthera* species.

Species	References
A. albida Griseb.	Borsch 1998
A. bettzickiana (Regel) G.Nicholson	Li et al. 1993
A. caracasana Kunth	Müller & Borsch 2005b
A. costaricensis Kuntze	Borsch 1998
A. filifolia (Hook.f.) Howell J.T.Howell	Borsch 1998
A. flavescens Kunth	Borsch 1998, Nowicke & Skvarla 1979
A. galapagensis (Stewart) J.T.Howell	Eliasson 1988
A. geniculata Urb.	Eliasson 1988
A. gracilis Loes.	Erdtman 1966
A. maritima (Mart.) A.St.-Hil.	Borsch 1998
A. nesiotes I.M.Johnst.	Eliasson 1988
A. nodiflora R.Br	Li et al. 1993
A. olivacea Urb.	Borsch 1998
A. paronychioides A.St.-Hil.	Perveen & Qaiser 2002
A. peruviana (Moq.) Suess.	Borsch 1998, Eliasson 1988
A. philoxeroides Griseb.	Li et al. 1993
A. pungens Kunth	Bashir & Khan 2003
A. reineckii Briq.	Eliasson 1988
A. repens Steud.	Mittre 1962
A. sessilis (L.) R.Br. ex DC.	Kajale 1940, Mittre 1962, Rao & Shukla 1975, Li et al. 1993, Liang et al. 1978, Perveen & Qaiser 2002

Pfaffia type. The pollen grains in this category are dodecahedric, metareticulate, tectate perforate with microspines distally arranged in a line. The apertures are pantoporate with pore structure of Type I (Borsch 1998). The diameter of the pores is 3–6 µm and is covered by 20–60 ektexinous bodies. The length of these ektexinous bodies is 1.5–3.0 times its width. These ektexinous bodies are rectangular, sinuous or elongated and are arranged in a mosaic-like pattern, closely adjoined but separated from each other. Each of the ektexinous bodies has one to four distinct microspines attached onto it.

Studies of *Alternanthera* in Malaysia date back to the 18th century when Ridley (1924) reported *A. sessilis* in the Malay Peninsula. *Alternanthera sessilis* (L.) R.Br. ex DC., *A. sessilis* var *tenuissima* (Suess.) Backer, *A. repens* Kuntze, *A. bettzickiana* (Regel) G.Nicholson, *A. philoxeroides* Griseb., *A. brasiliana* (L.) Kuntze and *A. porrigens* Kuntze from Malesia were subsequently described (Backer 1949). *Alternanthera triandra* Lamk. has been recorded as a common weed in Malaya. However, in Turner's catalogue of Malayan Plants (1995), only three species (*A. sessilis, A. philoxeroides* and *A. bettzickiana*) were recognised. Of these, the pollen grains of three species were investigated in the present study, i.e., *A. sessilis* (both the red variety as well as the green, the later sometimes considered as a distinct species, *A. triandra* Lamk.), *A. bettzickiana* and *A. paronychioides*.

In Peninsular Malaysia, *A. sessilis* occurs in two leaf colours: green and red. Both the green and red varieties of *A. sessilis* are perennial creeping herbs. The red variety is commonly cultivated, whereas the green variety is a common weed found growing in various types of habitat from moist areas near drains, ditches and ponds to dry open wastelands. Similarly, *A. bettzickiana* is usually found in dry open wastelands or moist areas near ditches. However, these two species can be easily identified by the morphology of stem, leaf and flower (Table 2). Lastly, *A. paronychioides* could be found on dry sandy ground such as along canals or roads. This species forms a dense mat with numerous prostrate branches with roots at the nodes.

Alternanthera sessilis is regarded by some communities as a useful medicinal plant indigenous to Malesia. The red variety is usually used as a herb to treat heart disease and hypertension. Scientifically, *A. sessilis* has been reported to have antibacterial activities (Kumaresan et al. 2001, Jalalpure et al. 2008). Free radical scavenging properties have also been found in *A. sessilis* indicating the presence of antioxidant properties in the plant (Balasuriya & Dharmaratne 2007, Bhaskar et al. 2007, Shyamala et al. 2004). Other reported pharmacological activities of *A. sessilis* include reduction of hypertension (Goh et al. 1995), having an hepatoprotective effect against liver injuries induced by hepatotoxins (Song et al. 2006) as well as functioning as a diuretic (Goh et al. 1995). As the two varieties of *A. sessilis* are similar except in leaf colour, this study also aims to elucidate their pollen morphology to determine whether they differ.

Materials and methods

Pollen samples for the green and red varieties of *A. sessilis* were collected from Varsity Lake and the Rimba Ilmu Botanic Garden, respectively, in the University of Malaya, Kuala Lumpur. The pollen grains of *A. bettzickiana* were collected from the Forest Research Institute Malaysia (FRIM) and *A. paronychioides* from the Kuala Selangor Nature Park, Selangor, Peninsular Malaysia. Voucher specimens were deposited in the herbarium of the Institute of Biological Sciences, University of Malaya (KLU).

Anthers of 15 flowers of each species were collected after anthesis. The pollen samples were then acetolysed according to the standard procedure of Erdtman (1960). Slides for light microscopy (LM) study were prepared with glycerine jelly and sealed with wax. The measurements of equatorial diameter (E) and polar length (P) were taken with a Leica DM100 microscope. Then, the pollen shape and size were determined. Acetolysed pollen grains for scanning electron microscopy (SEM) study

Table 2. Morphological characters of *Alternathera sessilis* (green and red varieties), *A. paronychioides* and *A. bettzickiana*.

Species	Colour, habit and selected morphological traits					
	Stem	*Foliage*	*Flowers*			
			colour	petals	stamens	ovary
A. sessilis (green variety)	green tinged with purple at the node; ascending, creeping or decumbent	green; simple; opposite; narrowly elliptic or narrowly oblong	creamy white	5, subequal in size	3	compressed
A. sessilis (red variety)	red; decumbent or creeping	red; simple; opposite; variable, mainly narrowly elliptic or oblanceolate	red	5, subequal in size	3	compressed
A. paronychioides	green; prostrate and forming a mat	green; simple; opposite; thick cuticle; elliptic or obovate	creamy white	5, distinctly unequal in size	5	compressed
A. bettzickiana	green tinged with purple at the node; erect or ascending	green; simple; opposite; elliptic	creamy white	5, distinctly unequal in size	5	subconical

were coated with gold, examined and photographed using a JOEL JSM-6400 scanning electron microscope.

Terminology used generally follows that of Fægri & Iversen (1950), Erdtman (1952), Borsch (1998) and Borsch & Barthlott (1998). An independent samples t-test was conducted to compare the polar length, equatorial diameter, diameter of the pores and number of ektexinous bodies between the following: 1) the green and red varieties of *A. sessilis*. 2) the green variety of *A. sessilis* and *A. bettzickiana*. 3) the red variety of *A. sessilis* and *A. bettzickiana*. The analyses were performed using the SPSS version 11.5 for Windows.

Results

The SEM photomicrographs of pollen in polar view, equatorial view, and pore structure are shown in Fig. 1. The pollen grains of *Alternanthera* species are dodecahedric, isopolar and radially symmetrical (Table 3). The pollen grains are small (12.56–23.57 µm in length) with the average polar axis varying between 15.19 and 21.36 µm and the average equatorial axis 17.18–21.85 µm. The t-test (Table 4) indicated there was no significant difference in polar length [$t (98) = -1.35, p > 0.05$] and equatorial diameter [$t (98) = 1.32, p > 0.05$] of the green and red varieties of *A. sessilis*. For the green variety of *A. sessilis* and *A. bettzickiana*, the t-test indicated significant difference in the polar length [$t (86.58) = 3.12, p < 0.05$], but no significant difference in equatorial diameter [$t (98) = 1.76, p > 0.05$]. Similarly, the red variety of *A. sessilis* and *A. bettzickiana* are significantly different in polar length [$t (98) = 5.24, p < 0.05$] but not in equatorial diameter [$t (98) = 0.46, p > 0.05$].

Under the scanning electron microscope, the apertures of *A. sessilis* and *A. bettzickiana* are pantoporate with twelve round pores, whereas pollen grains of *A. paronychioides* have approximately eighteen oval pores. Each of the pores is situated in a pentagonal face which contributes to the dodecahedric body of the pollen grain. The green variety of *A. sessilis* possesses the smallest pore (4.17 µm), followed by the red variety of *A. sessilis* (4.48 µm), *A. bettzickiana* (4.83 µm) and *A. paronychioides* (6.06 µm). The result of the t-test shows that there is a significant difference in the pore diameter of both green and red varieties of *A. sessilis* [$t (58) = -3.86, p < 0.05$].

The average number of ektexinous bodies in the red and green varieties of *A. sessilis* is the lowest, 28 and 29 respectively, followed by *A. bettzickiana* (33) and *A. paronychioides* (36). The number seems to be related to the size of the pores. For instance, the pollen grains of *A. paronychioides* have the biggest pores (6.06 µm) and highest average number of ektexinous bodies (36). The t-test shows that there is no significant difference in the number of ektexinous bodies of the green and red varieties of *A. sessilis* [$t (17.82) = 1.67, p > 0.05$]. On the other hand, both varieties of *A. sessilis* and *A. bettzickiana* are significantly different in the number of ektexinous bodies, i.e., the green variety of *A. sessilis* and *A. bettzickiana* [$t (26) = -2.42, p < 0.05$], and the red variety of *A. sessilis* and *A. bettzickiana* [$t (16.86) = -4.53, p < 0.05$]. The length of the ektexinous bodies is 4–6 times its width. They are rectangular, sinuous or elongated and each of the ektexinous bodies has 3–4 distinct microspines attached onto it. These ektexinous bodies are arranged in a mosaic-like pattern, closely adjoined but separated from each other.

The sexine of the pollen grain is metareticulate with a row of microspines that are regularly and distally arranged. These microspines are cylindrically elongated and blunt. The average height of these microspines ranges from 0.22–0.45 µm. The pollen grains of all the species studied are tectum perforate with unevenly distributed perforations at the top and base of the mesoporia, except in the pollen grains of *A. bettzickiana*, in which the perforations are distributed unevenly at the top of the mesoporia only.

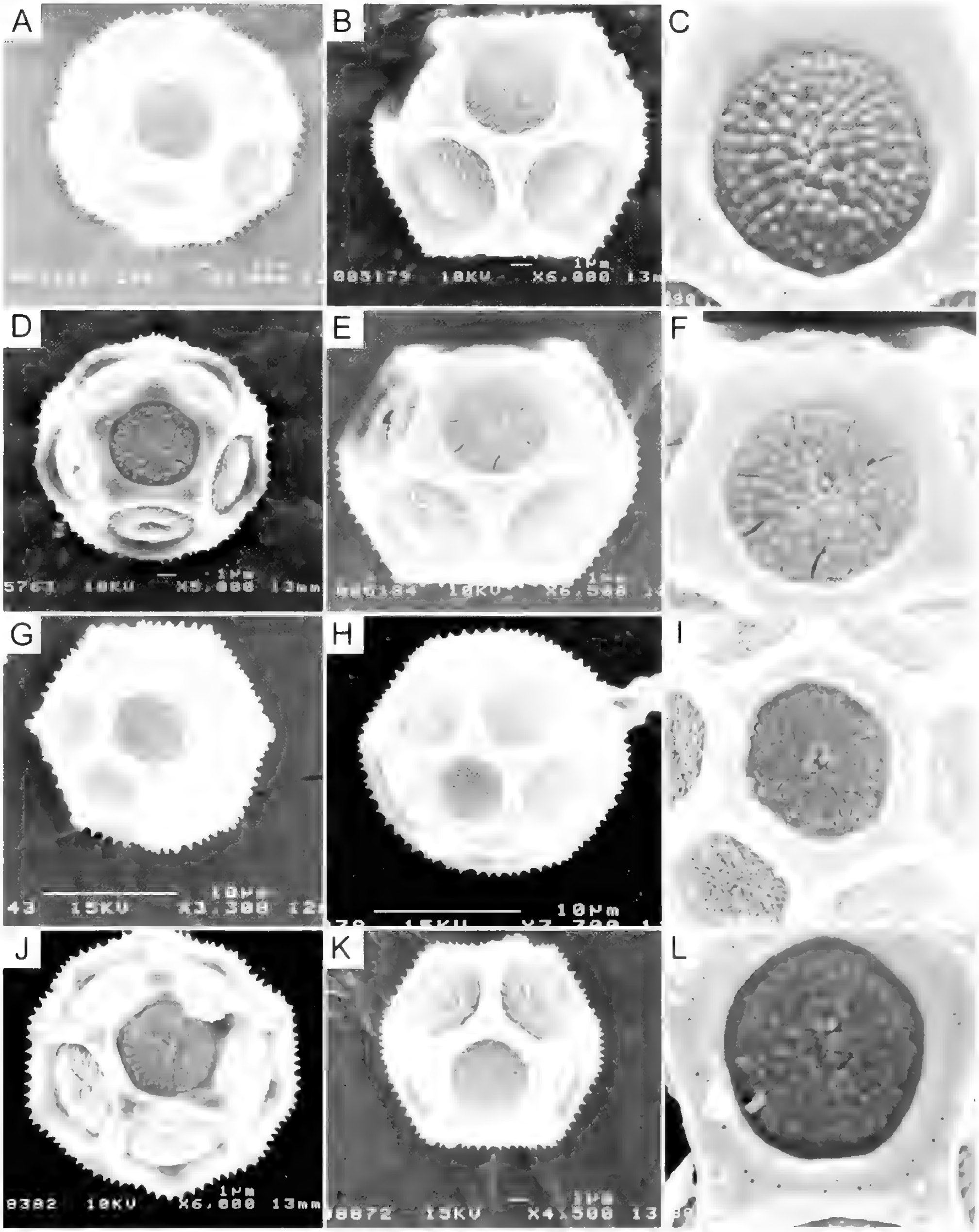

Fig. 1. SEM photomicrographs of pollen in polar view, equatorial view, and pore structure. **A–C.** *A. sessilis* (green variety); **D–F.** *A. sessilis* (red variety); **G–I.** *A. paronychioides* and **J–L.** *A. bettzickiana*.

Table 3. Pollen morphological characters of *A. sessilis* (green and red varieties); *A. paronychioides* and *A. bettzickiana* under LM and SEM. c, closely adjoined but separated; ce, cylindrically elongated; dr, distally and regularly arranged in a line; E, equatorial diameter; eb, ektexinous bodies; l, elongate; m, mosaic pattern; P, polar length; P/E, ratio between polar length and equatorial diameter; r, rectangular; s, sinuous; s.e., microspines attached on each of the ektexinous bodies.

Species				*A. sessilis*				*A. paronychioides*		*A. bettzickiana*
Characters				Green		Red				
Polarity				Isopolar		Isopolar		Isopolar		Isopolar
Symmetry				radially symmetrical		radially symmetrical		not symmetrical		radially symmetrical
Shape				dodecahedron		dodecahedron		dodecahedron		dodecahedron
Size										
	P(µm)		n 50	(12.56 -) 15.19 ± 1.19 (-18.04)	n 50	(13.67-) 15.48 ± 0.95 (-18.18)	n 18	(20.12 -) 21.36 ± 1.00 (-23.57)	n 50	(14.06-) 15.79 ± 0.84 (-18.04)
	E(µm)		n 50	(15.17 -) 17.94 ± 1.02 (-19.97)	n 50	(16.09-) 17.69 ± 0.82 (-19.66)	n 50	(20.40 -) 21.85± 2.65 (-23.53)	n 50	(14.78 -) 17.18 ± 1.40 (-21.97)
	P/E			0.85		0.88		0.98		0.92
	Class			small		small		small		small
Aperture				pantoporate		pantoporate		pantoporate		pantoporate
	Pore									
		number		12		12		18		12
		diameter(µm)	n 30	(3.58-) 4.17 ± 0.35 (-4.85)	n 30	(4.11-) 4.48 ± 0.28 (-5.14)	n 8	(4.44-) 6.06 ± 0.83 (-6.76)	n 12	(4.51-) 4.83 ± 0.20 (-5.12)
		eb								
		shape		l, r, s		l, r, s		l, r, s		l, r, s
		number	n 14	(23.00-) 29.40 ± 3.25 (-35.00)	n 14	(25.00-) 27.79 ± 1.48 (-30.00)	n 5	(32.00-) 35.80 ± 2.59 (-39.00)	n 14	(27.00-) 32.71 ± 3.79 (-40.00)
		s.e.		(2.52-) 3.23 ± 0.34 (-3.78)		(2.81-) 3.23 ± 0.27 (-3.70)		(3.27-) 4.38 ± 0.65 (-4.92)		(2.84-) 3.14 ± 0.26 (-3.59)
		length(µm)		(1.03-) 1.15 ± 0.10 (-1.38)		(1.10-) 1.28 ± 0.12 (-1.49)		(2.03-) 1.74 ± 0.19 (-1.54)		(1.12-) 1.26 ± 1.00 (-1.47)
		width(µm)		(0.20-) 0.26 ± 0.05 (-0.38)		(0.29-) 0.33 ± 0.03 (-0.39)		(0.27-) 0.31 ± 0.04 (-0.35)		(0.26-) 0.31 ± 0.03 (-0.36)
Sexine				metareticulum		metareticulum		metareticulum		metareticulum
Spines	height(µm)		n 30	(0.13-) 0.23 ± 0.04 (-0.40)	n 30	(0.15-) 0.22 ± 0.03 (-0.34)	n 23	(0.23-) 0.45 ± 0.04 (-0.59)	n 15	(0.19-) 0.29 ± 0.04 (-0.45)
	shape			ce		ce		ce		ce
	arrangement			dr		dr		dr		dr
Perforation	distribution			unevenly whole mesoporia		unevenly whole mesoporia		unevenly whole mesoporia		unevenly top mesoporia

Table 4. Independent samples t-test comparing the polar length (P), equatorial diameter (E), pore diameter and number of ektexinous bodies between *A. sessilis* and *A. bettzickiana*.

Species	Dependent variable	Levene's test for equality of variances		t-test for equality of means						
		F	*significance value*	*t*	*df*	*significance value (2- tailed)*	*mean difference*	*std. error difference*	*95% confidence interval of the difference*	
									Lower	Upper
A. sessilis both varieties	P (µm)	2.63	0.11	-1.35	98.00	0.18	-0.29	0.22	-0.72	0.14
	E (µm)	0.95	0.33	1.32	98.00	0.19	0.25	0.19	-0.12	0.61
	Pore diameter (µm)	1.69	0.20	-3.86	58.00	0.00	-0.32	0.08	-0.48	-0.15
	Number of ektexinous bodies	6.14	0.02	1.67	17.82	0.11	1.64	0.98	-0.42	3.71
A. sessilis (green variety) and *A. bettzickiana*	P (µm)	5.84	0.02	3.12	86.58	0.00	0.64	0.20	0.23	1.04
	E (µm)	1.45	0.23	1.76	98.00	0.08	0.32	0.18	-0.04	0.68
	Number of ektexinous bodies	0.39	0.54	-2.42	26.00	0.02	-3.29	1.36	-6.07	-0.50
A. sessilis (red variety) and *A. bettzickiana*	P (µm)	0.53	0.47	5.24	98.00	0.00	0.93	0.18	0.58	1.28
	E (µm)	0.05	0.82	0.46	98.00	0.65	0.07	0.16	-0.24	0.39
	Number of ektexinous bodies	10.68	0.00	-4.53	16.86	0.00	-4.93	1.09	-7.22	-2.63

The pollen morphology of the green and red varieties of *A. sessilis* is remarkably similar despite significant differences in their pore diameter. This difference alone is not sufficient to delimit them into two species. Furthermore, the pollen grains of these two varieties show no significant difference in polar length, equatorial diameter and number of ektexinous bodies.

Interestingly, the present study has shown that pollen grains of *A. bettzickiana* are almost identical to those of *A. sessilis*. Still, the pollen grains of these two species could be differentiated by significant difference in their polar length and number of ektexinous bodies. The pollen of *A. bettzickiana* is longer (*A. bettzickiana*: 15.79 μm; green and red varieties of *A. sessilis*: 15.19 μm and 15.48 μm, respectively) and the pore is covered by more ektexinous bodies (*A. bettzickiana*: 33; green and red varieties of *A. sessilis*: 29 and 28, respectively). Another character that differentiates these two species is the distribution of perforations. The perforations in *A. bettzickiana* are at the top of the mesoporia only whereas those from *A. sessilis* are around the whole mesoporia.

Clearly, the pollen of *A. paronychioides* is very different from the pollen of *A. sessilis* and *A. bettzickiana* in having around 18 oval pores while the other two species have only 12 round pores. The t-test could not be carried out to compare the polar length, pore diameter and number of ektexinous bodies between *A. paronychioides* and the other two species due to the difficulty in obtaining sufficient number of pollen grains from *A. paronychioides*.

Discussion

On the whole, pollen grains of the three species studied conform well to the *Gomphrena*-type of Erdtman (1966) which corresponds to the *Pfaffia* type of Borsch (1998). The pore structure is similar to the Type I of Borsch (1998). Similar observations have been reported in the pollen grains from the New World (Borsch 1998, Eliasson 1988, Müller & Borsch 2005b, Nowicke & Skvarla 1979) and China (Li et al. 1993, Liang et al. 1978) (Table 1). However, a few exceptions have been reported, i.e., *A. philoxeroides* (Li et al. 1993) and *A. costaricensis* Kuntze (Borsch 1998) are reported to have spheroidal pollen grains.

The present palynological results support existing data which have indicated that *Alternanthera* is stenopalynous in terms of pore number. Most of the species examined (Borsch 1998, Eliasson 1988, Li et al. 1993, Liang et al. 1978, Müller & Borsch 2005b, Nowicke & Skvarla 1979), including *A. sessilis* and *A. bettzickiana* in the present study, have 12–14 pores. Only a few exceptions were identified, such as 20–24 pores in *A. philoxeroides* (Li et al. 1993), 25–30 in *A. costaricensis* (Borsch 1998) and 18 in *A. paronychioides* (present study).

Compared with previous studies, the pollen grains of *A. sessilis* in the present study are distinctly different from those in Pakistan and India. For instance, the number of pores was reported as six in the grains of *A. sessilis* from the Upper Gangetic plain

(Rao & Shukla 1975) and 3–3.2 from Pakistan (Perveen & Qaiser 2002). In fact, the pollen of *A. sessilis* from India is reported to have granulated sexine ornamentation (Rao & Shukla 1975) and without spinules (Mittre 1962). However, this kind of apparent contradiction, especially the study from India, is difficult to resolve without further confirmatory work because the methodology and voucher specimens of *A. sessilis* were not mentioned by these authors and therefore taxonomic verification could not be carried out.

Further, the pollen grains of *A. bettzickiana* in the present study are different from those reported in China (Li et al. 1993) in having bigger pollen and pore (present study: polar length = 15.79 µm, pore: 4.83 µm) while those from China are smaller (polar length = 10.90 µm, pore = 3.60 µm). Moreover, only a single row of spinules are observed in the present study, whereas 1–2 rows of spinules are observed in the pollen from China.

In addition, data obtained in the previous study of *A. paronychioides* is different from the present findings. For instance, the pollen grains from Pakistan (Perveen & Qaiser 2002) were smaller (15.34 µm) with 6–9 pores while those from this study are bigger (21.85 µm) with around 18 oval pores. Furthermore, the size of the pores in the present study is about twice that of pores from the Pakistan pollen grains, i.e., 6.06 µm and 3.44 µm, respectively.

At the generic level, the pollen morphology of *Alternanthera* species is close to *Pfaffia* Mart. (Borsch 1998, Eliasson 1988), *Tidestromia* Standl. and *Kyphocarpa* Schinz in having dodecahedric pollen grains and metareticulate sexine (Borsch 1998). In fact, the current palynological data is generally in agreement with Borsch (1998) and thus might help in the genus delimitation. For instance, the pollen of *Alternanthera* can be distinguished from *Tidestromia* by the sexine pattern. The pollen of *T. lanuginosa* (Nutt.) Standl. is reported as devoid of spinules (Borsch 1998) and *T. oblongifolia* (S.Watson) Standl. has a very narrow mesoporia which is triangular in cross-section (Eliasson 1988). On the other hand, most of the *Alternanthera* species in the present study have one to two rows of microspines attached on the moderate mesoporia.

The number and shape of apertures appear to be an important key in differentiating the *Pfaffia* and *Alternanthera* species. Instead of having spheroidal grains with more than 20 pores as reported in *Pfaffia* (Borsch 1998), the pollen grains of *Alternanthera* are dodecahedric with less than 20 pores. Most of the *Pfaffia* species conform to the above characters except *P. aurata* (Mart.) T.Borsch, *P. completa* (Uline & W.L.Bray) T.Borsch, *P. costaricensis* (Standl.) T.Borsch and *P. densipellita* T.Borsch (Borsch 1995 & 1998). These species are reported also to have dodecahedric pollen with 12–14 pores and metareticulate sexine. However, the distribution of microspines on the sexine could be used to resolve this problem. The microspines are occasionally arranged in an undulate row or side by side, as seen in *P. aurata* and *P. costaricensis* (Borsch 1995) but distally and usually regularly arranged in most of the *Alternanthera* species.

Conclusion

Pollen grains of *A. sessilis*, *A. bettzickiana* and *A. paronychioides* in Peninsular Malaysia can be differentiated mainly by the number of apertures, number of ektexinous bodies and distribution of perforations at the mesoporia. The apertures of *A. sessilis* and *A. bettzickiana* are pantoporate with 12 round pores whereas the pollen grains of *A. paronychioides* have 18 oval pores. The sexine is metareticulate and tectum perforate with unevenly distributed perforations at the top and base of the mesoporia, except in the pollen grains of *A. bettzickiana*, in which the perforations are distributed unevenly at the top of the mesoporia only.

Although this study has indicated that the palynology of the green and red varieties of *A. sessilis* is remarkably similar, palynological data was only obtained from specimens at a single habitat. As the green-leafed variety of *A. sessilis* could be found from various habitats, e.g., in canals, ditches or wastelands, a survey on the pollen morphology from those habitats should also be carried out. Besides, future work should also include the transmission electron microscopy (TEM) study in order to strengthen the hypothesis that the pollen morphology of the green and red varieties of *A. sessilis* is not significantly different.

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Flower biology of four epiphytic Malesian Gesneriads

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ABSTRACT. Floral traits, flowering events, nectar production and reproductive success of *Aeschynanthus horsfieldii* R.Br., *A. pulcher* (Blume) G.Don, *A. longiflorus* A.DC. and *Agalmyla parasitica* C.B.Clarke were observed for sympatric populations in the Cibodas area, Mount Gede-Pangrango, West Java. All traits were significantly different among the species, but were associated with a bird pollination syndrome. Many flowers of *Aeschynanthus longiflorus* and *Agalmya parasitica* failed to develop mature stigmas. *Agalmyla parasitica* flowers take a longer time to attract pollinators and receive pollen than the others and the filaments begin to bend earlier than the others. *Aeschynanthus pulcher* produces more nectar than the other species at the female phase, but the concentration was lower than in *Aeschynanthus horsfieldii* and *Agalmyla parasitica*. These seem to be correlated with the reproductive success of the respective species, with flowers of *Aeschynanthus longiflorus* and *Agalmyla parasitica* setting fewer fruit than the other two species. Flower traits and pollination shift are discussed in light of evidence that *Aeschynanthus horsfieldii* also attracts bumble bees (*Bombus rucifes*).

Keywords. *Aeschynanthus*, *Agalmyla*, Gesneriaceae, flower biology, Malesia, pollination

Introduction

Among 28 genera of Gesneriaceae that occur in Malesia, only *Aeschynanthus* Jack and *Agalmyla* (Blume) G.Don have epiphytic representatives. *Aeschynanthus* comprises approximately 160 species, while *Agalmyla* has about a hundred. The distribution areas of these two genera overlap: *Agalmyla* (Hilliard & Burtt 2002) seems to be restricted to Malesia and its distribution nested within that of *Aeschynanthus* (Mendum et al. 2001), a genus that is also significant outside of the region (e.g., Middleton 2007, 2009).

With a lack of direct observation of pollinators for every plant species, pollination syndromes are usually inferred. However, Ollerton et al. (2009) and Merxem et al. (2009) have recently cautioned that presumed pollination syndromes do not always successfully predict the actual pollinators. Based on flower characters, *Aeschynanthus* and *Agalmyla* have the characteristic association with bird pollination. There is evidence that flowers of *Aeschynanthus longiflorus*, *A. pulcher* and three other species of *Aeschynanthus* are usually visited by both *Arachnothera* spiderhunters and sunbirds (Leeuwen 1937, McClure 1966). *Agalmyla* flowers have also been noted as bird-visited (Hilliard & Burtt 2002). The nectar content of *Aeschynanthus* flowers have the strength associated with bird pollination (Freeman et al. 1991).

This paper compares the phenotypic traits of flowers of four plant species from the presumedly bird-pollinated genera *Aeschynanthus* and *Agalmyla*, in view of evidence for bee-pollination in one of the species, *Aeschynanthus horsfieldii*.

Material and methods

The epiphytic Gesneriaceae species studied were *Aeschynanthus horsfieldii* R.Br. (section *Microtrichium*), *Aeschynathus longiflorus* A.DC. (uncertain sectional affiliation), *Aeschynanthus pulcher* (Blume) G.Don (section *Aeschynanthus*), and *Agalmyla parasitica* C.B.Clarke (section *Agalmyla*). All are widely distributed in West Malesia. The observations were carried out at Cibodas, on the northern slope of Mount Gede-Pangrango, West Java, from November 2009 to March 2010.

Flowers of these species were randomly tagged before they opened. For each tagged flower, the day of flower opening was recorded and the flower was harvested following 0, 1, 3, 5, 7, 10, and 13 days after opening. Some flowers, however, dropped before harvesting. The sample size for each harvesting time was 5–10 flowers. For each harvest time, the length of the calyx, corolla, flower tube, stamen, gynoecium; the width of the flower mouth; and the diameter of the stigma were measured using calipers (to ±0.05 mm). Planar projection and en-face areas were measured followed Dafni (1992).

The flowering event was observed using other flowers, with a sample size of 27–50 flowers per species. These flowers were observed every day from January to February, 2010. During this period and for each tagged flower, the day of flower opening, convexing of the stigma, curvature and wilting of the filament, and the corolla dropping, was recorded.

To observed nectar production, some sample flowers were bagged before their opening, using flipped plastic. Nectar was extracted from detached flowers using 50 µl micropipettes, at the staminate, sexual overlap and pistillate phases for each species. At each flower phase, nectar was extracted at four different times, 0700–0800 hrs, 1000–1100 hrs, 1300–1400 hrs, and 1600–1700 hrs. Sugar concentration in the nectar was measured for each flower using a portable sugar refractometer (Kenko Refractometer, 0–80 % Brix).

A whole shoot bearing flowers was monitored through making a “flower map” when it was difficult to individually tag every flower for observation. Flowers setting fruits were counted and the percentage fruitset of the total flower number observed was computed.

Results

Flower traits

Flower traits of the four study species are presented in Table 1. All flowers of observed taxa are red (e.g., Fig. 1). The calyces are free, divided to the base, except

Table 1. Flower traits of the four study species. Values are expressed as mean ± SD (with n, sample size, in brackets); those marked by the same superscripts in each row are not significantly different.

Flower trait	*Aeschynanthus horsfieldii*	*Aeschynanthus longiflorus*	*Aeschynanthus pulcher*	*Agalmyla parasitica*	Statistical analysis	
					F	*P*
Flower colour	red	red	red	red		
Calyx shape	free, divided to base	free, divided to base	cup-shaped	free, divided to base		
Flower attachment	pendent	erect	erect	erect		
Filament curvature	curled down	curled down	curled down	curled back		
Corolla length (mm)	27.99 ± 1.28^{a} (20)	81.58 ± 2.54^{d} (30)	63.95 ± 3.11^{c} (65)	43.78 ± 2.04^{b} (20)	1989.793	*<0.001*
Corolla tube length (mm)	22.03 ± 0.99^{a} (20)	74.84 ± 2.42^{d} (30)	49.49 ± 2.71^{c} (65)	36.33 ± 2.70^{b} (20)	2156.605	*<0.001*
Flower mouth width (mm)	7.98 ± 0.62^{a} (20)	14.63 ± 1.42^{c} (30)	16.29 ± 1.28^{d} (65)	12.48 ± 0.92^{b} (20)	266.055	*<0.001*
Filament length (mm)	26.88 ± 1.37^{a} (20)	95.11 ± 3.63^{c} (30)	63.11 ± 9.28^{b} (65)	64.45 ± 2.73^{b} (20)	284.820	<0.001
En-face area (cm^2)	0.90 ± 0.19^{a} (20)	2.17 ± 0.48^{b} (30)	4.42 ± 0.66^{c} (65)	1.049 ± 0.28^{a} (20)	394.289	<0.001
Profile planar area (cm^2)	1.71 ± 0.21^{a} (20)	6.89 ± 0.66^{d} (30)	5.45 ± 0.63^{c} (65)	3.85 ± 0.48^{b} (20)	425.266	<0.001
Ratio of profile planar to enface area	1.96 ± 0.35^{a} (20)	3.31 ± 0.83^{b} (30)	4.42 ± 0.66^{d} (65)	3.94 ± 1.28^{c} (20)	51.109	<0.001

for *Aeschynanthus pulcher*, which has a cup-shaped calyx. Flowers of *A. horsfieldii* are pendulous, while in the three others they are erect. The filaments of the three *Aeschynanthus* species are curled downwards, whereas those of *Agalmyla parasitica* are curled back. The longest corolla length, corolla tube length, and filament length are found in *A. longiflorus*. The widest flower mouth, en-face area, and ratio of profile planar to en-face ratio are found in *A. pulcher*.

Due to protandrous development, gynoecium length in all four species increased gradually after flower opening (Fig. 2). However, as much as 30.22 % (n = 225) of *Agalmyla parasitica* and 80.89% (n = 178) of *Aeschynanthus longiflorus* flowers failed to developed mature stigmas.

Fig. 1. Bumble bee (*Bombus rufipes* Lep.) visiting and pollinating flowers of *Aeschynanthus horsfieldii* R.Br.

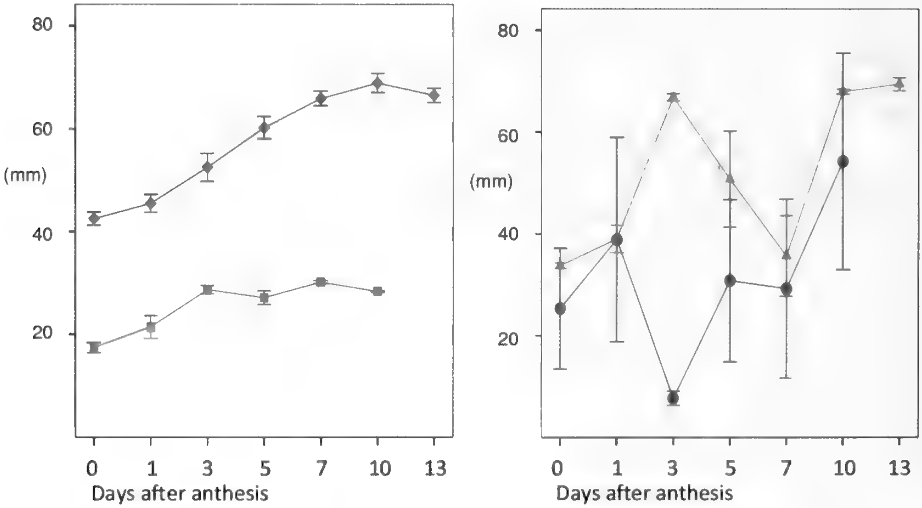

Fig. 2. Mean gynoecium length (±1 SE), in mm, of four species of Gesneriaceae after anthesis (flower opening): *Aeschynanthus pulcher* (◆), *A. horsfieldii* (■), *A. longiflorus* (●) and *Agalmyla parasitica* (▲). Note the horizontal axes are not to scale.

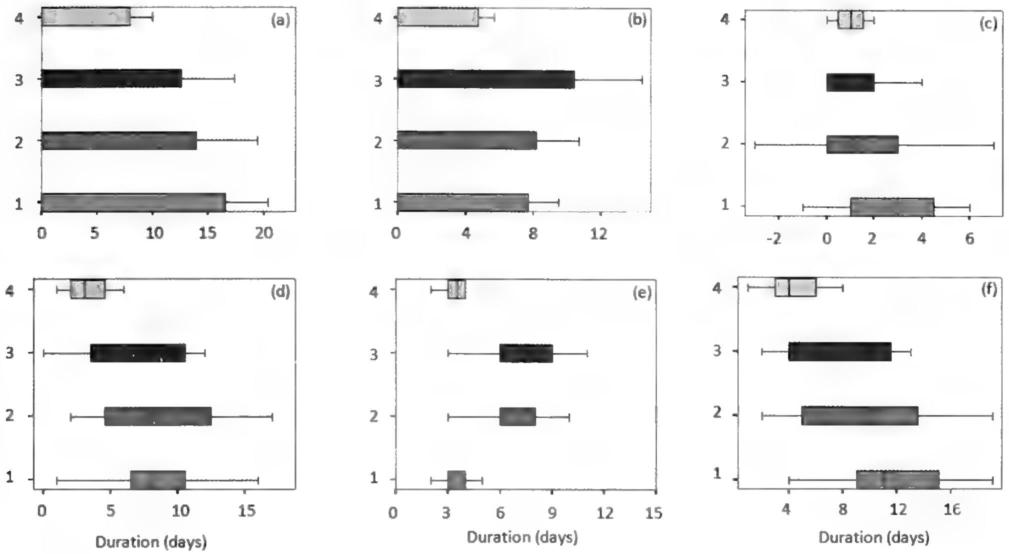

Fig. 3. Boxplots of the duration (in days) of (a) flower longevity, (b) male phase, (c) sexual overlap phase, (d) female phase, (e) filament curvature, and (f) stigma receptivity in *Aeschynanthus horsfieldii* (■ Bar 4 in each plot), *A. longiflorus* (■ Bar 3 in each plot), *A. pulcher* (■ Bar 2 in each plot) and *Agalmyla parasitica* (■ Bar 1 in each plot).

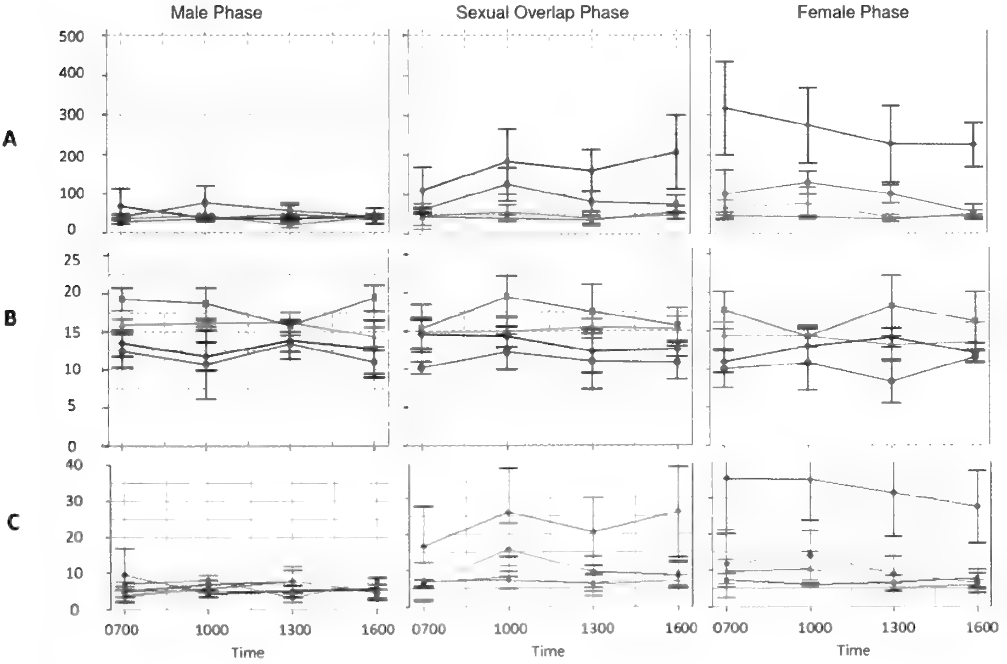

Fig. 4. Nectar volume (μl) (**A**), sugar concentration (% sucrose w/w) (**B**) and sugar amount (mg) (**C**) in *Aeschynanthus pulcher* (–), *A. horsfieldii* (–), *A. longiflorus* (–) and *Agalmyla parasitica* (–).

Flowering event

Characteristics of the flowering event (flower longevity, duration of the male and female phases, timing of filament curvature, and duration of stigma receptivity) are significantly different across the species, except the sexual overlap phase (i.e., when stamen functionality and stigma receptivity show an overlap), which showed weak differences (Fig. 3). The longest flower longevity was observed in *Agalmyla parasitica* ($F_{(3.145)}$=18.506, p<0.001). The longest male phase was found in *Aeschynanthus longiflorus* ($F_{(3.89)}$= 13.410, p<0.001), and the shortest female phase in *A. horsfieldii* ($F_{(3.86)}$=7.314, p<0.001). The duration of the overlap phase is only weakly different among the species ($F_{(3.83)}$=3.09; p<0.05). The sexual overlap phase is negative when the stigma becomes receptive after filaments have wilted, or when flowers do not display such overlap. The filaments of *A. longiflorus* were more slow to curve than in the three other species ($F_{(3.115)}$=16.955; p<0.001). The shortest stigma receptivity was observed for *A. horsfieldii* ($F_{(3.109)}$=15.667, p<0.001).

Flower nectar production

Nectaries of the four species are located at the flower base. In the *Aeschynanthus pulcher* flower, the corolla has a swollen (slightly bulbous) base which is not found in the other three species. The pattern of nectar production showed in Fig. 4. Nectar volume, and nectar sugar amount and concentration, vary over the time of day. There were also significant differences in nectar volume between the species and between flower phases, except in *A. horsfieldii* (Table 2).

The mean nectar sugar concentration was significantly different between species, but not between the flower phase in each species, except *Agalmyla parasitica* (Table 2). The highest nectar sugar concentration was found in *Aeschynanthus horsfieldii.*

The mean nectar sugar amount was significantly different between species in the overlap and female phases, but not in the male phase, when it was relatively minimal (Table 2). The mean nectar sugar amount was also significantly different between flower phases in *Aeschynanthus pulcher* and *A. longiflorus*, but not in *A. horsfieldii* and *Agalmyla parasitica*. The highest nectar sugar amount was found in *Aeschynanthus pulcher* flowers.

Reproductive success

More flowers of *Aeschynanthus pulcher* and *A. horsfieldii* successfully set fruit than in *A. longiflorus* and *Agalmyla parasitica* (Table 3). This unequal fruitset between the species could possibly indicate the presence of competition between species for pollinator services.

Discussion

According to conventional interpretation of pollination syndromes, bird pollination flowers have tubular shapes, are frequently red and odourless, and produce copious

Table 2. Nectar volume (μl), nectar sugar concentration (% sucrose w/w) and amount of sugar in nectar (mg) of *Aeschynanthus pulcher*, *A. horsfieldii*, *A. longiflorus*, and *Agalmyla parasitica*, during the male, sexual overlap and female phases of flowering. Values are means with standard deviations (SD) and sample size (n, in brackets) indicated.

Flowering Phase	Volume (μl)				Statistic	
	Aeschynanthus pulcher	*Aeschynanthus horsfieldii*	*Aeschynanthus longiflorus*	*Agalmyla parasitica*	F	P
Male (μl)	45.87±26.35 (20)	34.77±9.71 (20)	53.19±26.72 (20)	34.75±15.43 (20)	3.753	0.014
Overlap (μl)	164 .95±76.69 (20)	43.09±15.51 (20)	85.74±34.82 (20)	46.37±20.89 (20)	33.08	<0.001
Female (μl)	259.88±95.17 (20)	42.23±8.31 (20)	95.06±43.59 (20)	56.11±26.32 (20)	68.578	<0.001
Statistic	$F=44.13$; $p<0.001$	$F=3.108$; $p=0.052$	$F=7.574$; $p<0.01$	$F=5.014$; $p<0.05$		

Flowering Phase	Nectar sugar concentration (%)				Statistic	
	Aeschynanthus pulcher	*Aeschynanthus horsfieldii*	*Aeschynanthus longiflorus*	*Agalmyla parasitica*	*F*	*p*
Male (%)	12.96±2.48 (20)	18.28±2.06 (20)	11.87±2.7 (20)	15.61±1.22 (20)	34.24	<0.001
Overlap (%)	13.41±2.02 (20)	16.96±3.18 (20)	11.05±2.37 (20)	15.11±1.59 (20)	22.57	<0.001
Female (%)	12.49±1.91 (20)	16.57±3.25 (20)	10.14±2.68 (20)	13.79±1.93 (20)	22.80	<0.001
Statistic	$F=0.9$; $p=0.412$	$F=1.936$; $p=0.154$	$F=2.22$; $p=0.118$	$F=6.85$; $p=0.002$		

Flowering Phase	Nectar sugar amount (mg)				Statistic	
	Aeschynanthus pulcher	*Aeschynanthus horsfieldii*	*Aeschynanthus longiflorus*	*Agalmyla parasitica*	F	P
Male (mg)	6.14±4.29 (20)	6.52±2.21 (20)	5.97±2.17 (20)	5.48±2.66 (20)	0.41	0.742
Overlap (mg)	22.49±11.23 (20)	7.35±3.42 (20)	10.06±5.58 (20)	7.06±3.35 (20)	23.58	<0.001
Female (mg)	32.27±11.69 (20)	6.91±1.85 (20)	10.31±6.55 (20)	7.75±3.58 (20)	59.37	<0.001
Statistic	$F=37.15$; $p<0.001$	$F=0.519$; $p=0.598$	$F=4.53$; $p=0.015$	$F=2.59$; $p=0.083$		

Table 3. Percentage fruitset of *Aeschynanthus pulcher*, *A. horsfieldii*, *A. longiflorus* and *Agalmyla parasitica*.

Species	No. of flowers	No. of fruits set	% fruitset
Aeschynanthus pulcher	247	82	33.19
Aeschynanthus horsfieldii	117	40	34.18
Aeschynanthus longiflorus	178	23	12.92
Agalmyla parasitica	225	50	22.22

amounts of nectar, with the stigma and anthers conspicuously exserted from the floral tube. Although the flowers of all four species of Gesneriaceae observed have this classic bird pollination syndrome, the flowers of *Aeschynanthus horsfieldii* were frequently visited by bumble bees (*Bombus rupifes* Lep.) and could be said to show a shift in floral presentation.

Shifts in flower traits in *A. horsfieldii* may include the shallower flower tube length, narrower side advertisement, shorter flower longevity and higher nectar sugar concentration. With a shallower flower tube length, the nectar is more easily foraged by bees. The reduced flower tube length also decreases the potential effectiveness of side advertisement (profile planar area). According to Dafni (1994), there are little differences in the degree of side advertisement between bird flowers and large bee flowers. Primack (1985) and Stratton (1989) have also shown that bee flowers have shorter longevity than bird flowers. In *Sinningiae* (Gesneriaceae), bee flowers also have higher nectar sugar concentration than bird flowers (Perret et al. 2001).

All four species observed have red flowers, although only *A. horsfieldii* appeared to attract bumble bees. We do not know how the red colour in *A. horsfieldii* flowers is compatible with bee vision, and suggest that perhaps flowers of *A. horsfiledii* could have UV reflectance properties. Flowers which have red colour with UV reflectance can attract bees (Chitka & Waser 1997).

In terms of reproductive success, the existence of co-flowering species with similar syndromes should increase inter-specific competition and reduce pollination success (Sargent & Ackerly 2008, Chitka & Shürkens 2001). We suggest that each of the four related species could have developed a different strategy to attract pollinators. *Aeschynathus pulcher* has developed flowers with large side advertisement and which produce high nectar volume and nectar sugar amounts. *Aeschynathus horsfieldii* has flowers able to attract more than one pollinator class (birds and bumble bees) through narrow side advertisement, high nectar sugar concentration and probably both nectar and pollen as rewards.

Aeschynanthus longiflorus and *Agalmyla parasitica* could have a "flower dimorphism syndrome", sometimes apparently showing andromonoecy, when some plants only present flowers with undeveloped gynoecia (i.e., with functionally male flowers), while others present the usual hermaphrodite condition. From a population perspective, producing more male flowers is a strategy to increase pollen transfer when there are limitations in plant resources and pollinator visitation.

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The genus *Premna* (Lamiaceae) and the presence of 'pyro-herbs' in the Flora Malesiana area

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ABSTRACT. The genus *Premna* consists of 14 species in the Flora Malesiana area. The most common species in the region are all widespread. However, a series of morphologically closely-related, rare and generally geographically more restricted species are present in the region. These species can be characterised by three distinct morphological characters: 1) small decussate scales at the base of the young twigs, 2) a calyx that always has four isomorphic lobes, 3) a fruit that is clavoid in shape and almost single-seeded. The ecology and morphology of *Premna herbacea* Roxb. is unique in the genus and is the first recognised 'pyro-herb' in the Flora Malesiana area.

Keywords. Lamiaceae, Malesia, *Premna*, pyro-herbs

Introduction

The genus *Premna* was first described by Linnaeus in 1771 and occurs in the old world tropics from Africa to China and south to Australia and the Pacific (Harley et al. 2004). Following most other genera in the Lamiaceae, *Premna* is rich in species and morphological variation on the Southeast Asian mainland and on the islands of the Sunda shelf. It is widespread in the Pacific, but the number of species decreases sharply south and east from New Guinea. Eighty percent of all *Premna* specimens in K belong to only four species (*P. serratifolia, P. odorata, P. trichostoma* and *P.tomentosa*) and these are all widespread. There are two groups of species in this genus. The first group (*P. serratifolia*-group, see Table 1) has most of these common species: (*P. serratifolia, P. odorata* and *P. tomentosa*), while species in the second group tend to be rare and generally geographically more restricted (*P. trichostoma* group, see Table The difference between the groups is mainly based on three distinct morphological characters. The *P. trichostoma*-group has a series of small decussate triangular scales at the base of the young twigs, while on older branches these scales usually have fallen off, leaving a series of closely packed bract scars; a calyx that always has four isomorphic lobes, its shape remaining largely intact when the flower develops and when the fruits are formed; and a fruit that is clavoid in shape, almost single seeded (four seeds present, but only one fully developing). While the *P. serratifolia*-group

Table 1. Species of *Premna* in the Flora Malesiana area and their distribution in each morphological group.

Taxon	Distribution
***P. serratifolia*-group**	
P. odorata Blanco	India and China to Australia
P. pubescens Blume	Java, Sumatra, the Lesser Sunda Islands and the Philippines
P. serratifolia L.	East Africa to Tahiti
P. sterculiifolia King & Gamble	Peninsular Malaysia
P. tomentosa Willd	India and China to Australia, except Borneo
***P. trichostoma* group**	
P. clavata de Kok	Sabah
P. decurrens H.J.Lam	Sumatra
P. herbacea Roxb.	Southeast Asia to Australia
P. interrupta Wall. Ex Schauer	India and China to Malaysia
P. oblongata Miq.	Sunda Islands and Sulawesi
P. pallescens Ridl.	Borneo
P. parasitica Blume	Java and Bali
P. regularis H.J.Lam	Philippines and New Guinea
P. trichostoma Miq.	Myanmar and Vietnam to New Guinea

does not have these bracts at the base of the young shoots, the number of calyx lobes varies from 0 to 5 and are almost always heteromorphic, and the fruits have four mature seeds per fruit.

The ecology and the morphology of *P. herbacea* is of interest. The herbaceous habit of this species is an illusion, as only the herb like twigs are visible above ground (and are usually the only parts collected), but a short woody stem exists below or near to the ground. *Premna herbacea* is in gross-morphological and ecological terms very similar to the well known 'pyro-herbs', which occur in vegetation types adapted to frequent fires. Given the many notes on herbarium labels stating that this species occurs in vegetation which is frequently burned, the same factor may have been the driving force behind the evolution of *P. herbacea*.

Pyro-herbs

Pyro-herbs are woody plants that survive frequent fires by reducing their woody parts to underground structures and then only sprout herb-like branches each year in the wet season. They are very common in parts of Tropical Africa and South America and are rare in Asia. They are reported to be absent from Australia and South East Asia (White 1976). Since White's overview article on pyro-herbs (or the suffrutescent habit), their presence has been indentified in north Australia. At least three species belonging to the Labiatae are now recognised to be pyro-herbs (*Clerodendrum tatei* (F.Muell.) Munir and *Clerodendrum linifolia* (Ewart & B.Rees) de Kok and *Premna herbacea* Roxb. Given that the two essential elements of recognising a plant as a pyro-herb is the woody underground parts (seldom present in herbaria) and a fire-regulated ecology (seldom mentioned on herbarium labels), pyro-herbs are difficult to recognise without extensive fieldwork. The case of *C. linifolia* shows clearly the difficulty of recognising these kinds of plants from herbarium material only. The species was first described as a monotypical genus *Huxleya* in the then also most entirely woody family Verbenaceae. The main reason that it was described as a new genus was because the type specimen consisted of only the herbaceous above-ground branches. This misconception lasted until more detailed morphological, ecological, chemical and molecular research revealed the true phylogenetic relationship of the genus and its survival strategy in a habitat that burns almost annually (de Kok et al. 2000, Steane et al. 2004). Similar ecological observations have now been made for the Australian populations of *P. herbacea* (Munir 1984; de Kok, in press).

Absence or presences of pyro-herbs in Southeast Asia

There is not much literature about pyro-herbs in Southeast Asia. In his papers on the ecology of the Indramajoe plains in West Java, van Steenis (1936) mentioned some possible examples (see Table 2). On the other hand, White (1976) reports them to be absent from South East Asia, and Henty (1982) mentions some possible examples from Papua New Guinea from what he calls 'the short lowland grasslands' which are maintained by frequent fires.

Conclusions:

1) The 14 species of *Premna* in the Flora Malesiana area can be divided into two distinct groups: the *P. trichostoma* and *P. serratifolia* groups, based on morphological characters.

2) *Premna herbacea* Roxb is the first recognised 'pyro-herb' in the genus in the Flora Malesiana area.

Table 2. Possible 'pyro-herbs' occurring in Southeast Asia.

Taxa	Sources
Butea monosperma (Lam.) Taub	Van Steenis 1936
Crotalaria alata Buch.-Ham. ex D.Don	Henty 1982
Crotalaria ferruginea Scheele	Henty 1982
Crotalaria montana B.Heyne ex Roth	Henty 1982
Dillenia sp.	Van Steenis 1936
Fordia fruticosa Craib	Van Steenis 1936
Grewia sp.	Van Steenis 1936
Morinda sp.	Van Steenis 1936
Phyllanthus emblica L.	Van Steenis 1936
Premna herbacea Roxb.	de Kok, in press
Ziziphus sp.	Van Steenis 1936

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A preliminary study on *in vitro* seed germination and rooted callus formation of *Tetrastigma rafflesiae* (Vitaceae)

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ABSTRACT. *In vitro* seed germination and induction of rooted callus formation was investigated as a preliminary study on the propagation of *Tetrastigma rafflesiae* as potential host plant material towards a sustainable conservation effort for *Rafflesia*. Seed germination of *T. rafflesiae* is epigeal with seedling emergence ranging 30–60 days after planting (dap), regardless of light presence. After 60 days, 54–60% of seeds germinated in media treatments. Callus formation began 7 dap in MS medium + 2 mg/L NAA, and 21 dap in MS medium + 2 mg/L 2,4-D. Browning of this medium due to phenolic compounds resulted from cutting a part of the hypocotyl. Rooting of the callus was obtained after 21 days on MS medium + 2 mg/L NAA, but was not evident with addition of 2 mg/L 2,4-D.

Keywords. *In vitro* seed germination, *Tetrastigma rafflesiae*, rooted callus

Introduction

Tetrastigma (Miq.) Planch. (Vitaceae) includes c. 100 species throughout tropical and subtropical areas, in Asia and northern Australia. Some of those species are traditionally used for medication in Indonesia and Malaysia, especially as leaf poultice in treating fevers and headaches. In the Philippines, *Tetrastigma* is used to cure scabies. In Vietnam, the leaf extract is used either internally or externally to treat headaches and fevers. In addition, the fruits of some species can be eaten (Lemmens 2003).

Tetrastigma is also well known as the exclusive host of the parasitic *Rafflesia* R.Br. (Nais 2001). Most *Rafflesia* spp. in Sumatra subsist parasitically on *Tetrastigma rafflesiae* (Miq.) Planch., of which *T. leucostaphylum* (Dennst.) Alston ex Mabb. is a synonym; see Veldkamp (2008). A shortage of the host plant caused by, for example, habitat reduction, can potentially affect the natural establishment and survival of *Rafflesia* spp. (Attenborough 1995, Meijer 1997). The seriously damaged forest environment in Sumatra makes it likely that viable *Rafflesia* populations remain only in some protected areas (Zuhud et al. 1999, Sofiyanti et al. 2007). It may be possible to help preserve the existence of *Rafflesia* in Sumatra by carrying out *in vitro* propagation of the host plant, so that host-plant abundance and sites can be potentially increased.

As far as we know, there have been no reports about *in vitro* propagation of *Tetrastigma*. Tissue culture techniques for *Tetrastigma* can potentially be adapted from those used for the better investigated commercially important *Vitis* L. *In vitro* propagation of *Vitis*, particularly grape, has been commercially carried out since a long time ago (Akbas et al. 2004, Salami et al. 2005, Alizadeh et al. 2010). Jaskani et al. (2008) added the auxin NAA (approximately 2 mg/L) to the Murashige-Skoog (MS) medium to induce rooted callus and embryo formation from grape leaf tissue.

This preliminary study aims to investigate the period of seed germination of *T. rafflesiae* on various media preparations, and the optimal conditions for *in vitro* seed germination. It also attempts to induce rooted callus from pieces of hypocotyls by using different types of auxin.

Materials and methods

Tetrastigma rafflesiae fruits were collected from the Andalas Botanical Garden for use as an explants source.

The Murashige–Skoog (MS) basic medium was used, to which was added modified active carbon, kinetin, NAA (1-Naphthalene Acetic Acid), or 2,4-D (2,4-Dichlorophenoxyacetic acid), as required. Other substances added included 0.7% agar and 3% sucrose. The culture medium acidity was controlled at pH 5 ± 0.5. The culture medium was heated until it boiled before being poured into sterilised culture bottles. The bottles were then covered with aluminum foil and paper and secured with rubber bands. Culture bottles were autoclaved for 15 minutes at 121°C and 15 psi pressure.

Ripe fruits of T. *rafflesiae* were sterilised by soaking in 5% commercial detergent solution for 20 minutes and washing them in flowing water for 5 min. The fruits were then rinsed with 70% alcohol for 5 min, then commercial bleach (30%) with 2 drops of Tween 20 for 5 minutes, before being washed three times with sterile distilled water. Fruits were then peeled and seeds extracted and sterilised with 70% alcohol for 3 min, and with 10% hypochlorite mixed with 1 drop of Tween 20 for 3 min before finally being washed with sterile distilled water for 5 min. These sterilised seeds were then ready for implantation into the treatment media.

For *in vitro* seed germination experiments, *T. rafflesiae* seed was germinated on four media types: basic MS medium, MS + 1 g/L active carbon, MS + 0.5 mg/L kinetin and MS + 0.5 mg/L kinetin + 1 g/L active carbon. The seed-implanted culture media were then placed in two environments, a controlled incubation room (24°C ± 2°C) with alternate 12 hours lighting (1000–1500 Lux), and a dark room. Type of seed germination, period (range in days) of germination, and percentage germination were recorded.

To study the effect of two types of auxin on *in vitro* induction of rooted callus from excised hypocotyls of *T. rafflesiae*, the hypocotyls were cut and implanted on two types of media to induce rooted callus formation. Media employed were MS + 2 mg/L NAA + 0.5 mg/L kinetin, and MS +2 mg/L 2,4-D + 0.5 mg/L kinetin. The culture media with hypocotyls were placed in a room with 12 hours lighting and in a dark room, for 2 weeks, to induce callus formation. The time of callus formation, time of rooted callus formation, type and colour of callus, and percentage of callus and rooted callus formation, were recorded.

Results and discussion

In vitro seed germination of Tetrastigma rafflesiae

Absence of light during germination did not affect the period of germination. However, phenolic formation on the treatment media was higher in the presence of light (Fig. 1 A–B).

The type of seed germination is epigeal in which the hypocotyl is elongated and the cotyledons are raised above the growth substrate (Fig. 1). The plants with this type include cucumber, cotton, sesbania (Tischler et al. 2000), sunflower, pea and flax (Klicova et al. 2004).

Table 1 shows that the time taken to first germination is 30 days after being implanted on the medium for all treatments. The seed that germinated the highest was seen on the MS medium with 0.5 mg L kinetin added. Thus kinetin is capable of promoting seed germination. Conversely, the lowest seed germination was seen on the MS medium without growth regulators added; statistical significance, however, was not tested in this preliminary trial.

The addition of active carbon does not affect the growth medium except that it can reduce phenolics production by the explants. However, the phenolic compounds produced do not appear to affect the *in vitro* seed germination of *T. rafflesiae*. Klicova et al. (2004) assert that sunflower seed germination requires cytokinin-type growth regulators to induce growth of the shoot with the use of 0.12% BA (6-benzyladenin).

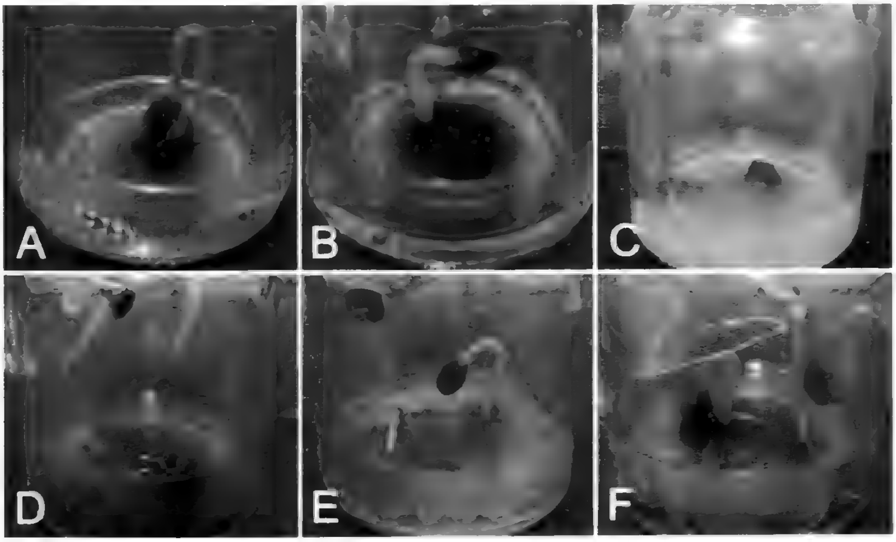

Fig. 1. *Tetrastigma leucostaphylum* seed germination in two environmental conditions in MS basic medium, after 8 weeks of treatment (A–B); and on four types of media with alternate 12-hours lighting, after 60 days (C–F). **A.** Complete darkness. **B.** Alternate 12-hours lighting. **C.** MS basic medium. **D.** MS + 1 g L active carbon. **E.** MS + 0.5 mg L kinetin. **F.** MS + 1 g L active carbon + 0.5 mg/L kinetin. Photo by M. Idris.

Table 1. Time of seed germination (days after planting (dap) in the medium) and percentage germination after 60 days, in alternate 12 hours lighting.

No	Treatment	Germination (dap)	% Germination	Tissue formation / medium
1	MS	30–55	54	roots formed, cotyledons raised, hypocotyls elongated / medium became brown
2	MS + 0.5 mg/L kinetin	30–54	60	roots formed, cotyledons raised, hypocotyls elongated / medium became brown
3	MS + 1 g/L active carbon	30–52	56	roots formed, cotyledons raised, hypocotyls elongated / medium normal
4	MS + 1 g/L active carbon + 0.5 mg/L kinetin	30–52	56	roots formed, cotyledons raised, hypocotyls elongated / medium normal

Table 2. Period (days after planting, dap) and percentage of callus and rooted callus formation.

Treatment	Period of callus formation (dap)	Period of rooted callus formation (dap)	% Callus formation	% Rooted callus formation
MS + 2 mg/L NAA + 0.5 mg/L kinetin	7–10	21–30	100	80
MS + 2 mg/L 2,4-D + 0.5 mg/L kinetin	15–21	(nil)	100	0

Auxins and rooted callus induction from excised T. rafflesiae hypocotyls

MS medium augmented with 2 mg/L NAA was more effective at inducing rooted callus formation compared to the MS medium with 2 mg/L 2,4-D (Table 2). In the NAA-augmented medium, the elongation process and callus formation already began just 7 days after planting, and rooted callus formation began after 21 days after planting. Meanwhile, in the 2,4-D-augmented medium, there was browning and the tissue in fact shrank, and there was no sign of root formation (Fig. 2).

Jaskani et al. (2008) showed that addition of 2 mg/L NAA to the MS basic medium promoted callus formation and rooted callus formation from grape leaf tissue.

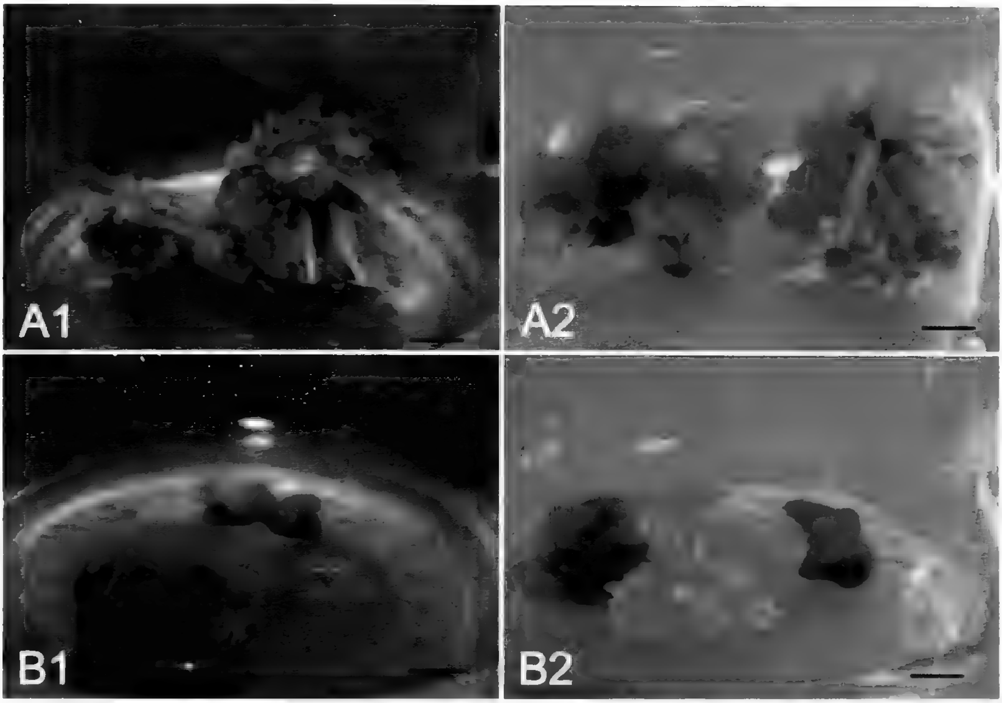

Fig. 2. Formation of rooted callus on excised *Tetrastigma leucostaphylum* hypocotyls in different media. MS + 2 mg/L NAA + 0.5 mg/L kinetin at 30 (**A1**) and 60 (**A2**) days after planting, dap; and MS + 2 mg/L 2,4-D + 0.5 mg/L kinetin at 30 (**B1**) and 60 (**B2**) dap. Scale bar = 0.5 cm. Photo by M. Idris.

Xu et al. (2005) added 1 mg/L 2,4-D to promote grape callus formation, but this did not initiate root formation. They also added 1 mg/L NAA and 0.25 mg/L BA which also formed callus without root formation. Akbas et al. (2004) added 1 mg/L NAA to the medium to induce shoot formation of grape.

Such rooted callus formation derived from *in vitro* manipulation can be a source of material to propagate the host plants of *Rafflesia*, and with which to investigate *in vitro* infection by *Rafflesia*. Zhou et al. (2004) used *Brassica napus* L. as an *in vitro* host material for infection by parasitic *Orobanche* L.. Kusumoto et al. (2007) used the root of *Trifolium pratense* L. for infection by *Orobanche minor* Sutton in their studies of the interaction between parasitic and host.

Conclusions

The basic MS medium augmented with 0.5 mg/L kinetin was effective in promoting *in situ* seed germination of *Tetrastigma rafflesiae*. The formation of rooted callus can be produced on MS medium by adding 2 mg/L NAA + 0.5 mg/L kinetin.

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Comparative anatomy of Grammitidaceae genera in Peninsular Malaysia

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ABSTRACT. Grammitidaceae is represented by 12 genera and 52 species in Peninsular Malaysia. The rhizome morphology and anatomy of Peninsular Malaysian Grammitidaceae were studied to determine whether it can be used as a supplementary character in generic delimitation. Two types of rhizome (creeping dorsiventral or erect), three types of stipe arrangement on the rhizome (in horizontal rows, in whorls or spiral) and two types of stele (solenostele or dictyostele) were identified.

Keywords. Anatomy, Grammitidaceae, morphology, Peninsular Malaysia, rhizomes

Introduction

Grammitidaceae is an important family for rainforest biodiversity in tropical montane regions with over 750 species worldwide (Parris 2003, 2010). For Peninsular Malaysia, 12 genera, namely, *Acrosorus* Copel., *Calymmodon* C.Presl, *Chrysogrammitis* Parris, *Ctenopterella* Parris, *Dasygrammitis* Parris, *Oreogrammitis* (Copel.) Parris, *Prosaptia* C.Presl, *Radiogrammitis* Parris, *Themelium* (T.Moore) Parris, *Tomophyllum* (E.Fourn.) Parris, *Scleroglossum* Alderw. and *Xiphopterella* Parris and 52 species are currently recognised (Parris 2007, 2010). Lately, the morphological and molecular aspects of this family have been intensively studied (Ranker et al. 2003, 2004; Schneider et al. 2004).

The Grammitidaceae have been treated in various ways taxonomically. Tryon and Tryon (1982) treated the entire Grammitidaceae as a single genus based on spore and sporangial characters while others established natural groupings based on the type of the rhizome, rhizome scales, stipe and rachis, types of frond hairs, venation patterns, soral arrangement and sporangial ornamentation (Parris 1983, 1986, 1995, 1997, 1998; Ranker et al. 2004). Parris (1995) also pointed out that neither cladistic nor cytological studies were helpful in the generic inter-relationships in the family; reticulate evolution possibly is one of the causes of failure.

For Peninsular Malaysia, all previous studies on this family were mainly based on morphological characters, ecology and phytogeography (Holttum 1955; Parris 1986, 1995, 1997, 1998, 2001, 2003, 2007, 2010). Rakotondrainabe & Deroin (2006) have shown that rhizome anatomy is a useful character in generic delimitation and can improve understanding of phylogeny of the family. Hence a study on rhizome anatomy of selected species of Grammitidaceae in Peninsular Malaysia was conducted in order to determine whether it can be used as a supplementary character in generic delimitation.

Material and methods

Fresh specimens of the rhizome were used for anatomical study. A list of specimens used is attached in Appendix A. Transverse sections 25–50 μm thick were made using the sliding microtome following the methods used by Sass (1958). These sections were stained with safranin and alcian green, then mounted with euparal. Anatomical data analysis was made with a Leica Diaplan microscope equipped with a CCTV camera. The photomicrographs were obtained from the camera through a computer using the Analysis software.

Results and discussion

Out of the 12 genera of the Grammitidaceae in Peninsular Malaysia, 11 were studied. The genus *Chrysogrammitis* Parris was excluded due to the limitation in obtaining fresh specimens. Two types of rhizome, three types of stipe arrangement and two types of vasculature were identified in this study (Table 1).

Two types of rhizome were observed, i.e., creeping dorsiventral and erect. Creeping dorsiventral rhizomes were found in *Ctenopterella* (Fig. 1: A1), *Dasygrammitis* (Fig. 1: A2), *Oreogrammitis* (Fig. 1: A3), *Prosaptia* (Fig. 1: A4) and *Themelium* (Fig. 1: A5) while erect rhizomes occur in *Acrosorus* (Fig. 2: A1), *Calymmodon* (Fig. 3: A1), *Radiogrammitis* (Fig. 2: A2), *Scleroglossum* (Fig. 3: A3 & A4), *Tomophyllum* (Fig. 2: A3) and *Xiphopterella* (Fig. 3: A4). In comparison with Hovenkamp (1990), the results in the current study agreed with the creeping dorsiventral type of rhizome in *Prosaptia*. However for *Dasygrammitis*, instead of the radial type of rhizome found by Hovenkamp (1990), the current study found only the creeping dorsiventral type of rhizome for both *D. brevivenosa* and *D. fuscata*.

Three types of stipe arrangement were found in this study:

1) In horizontal rows, which occur in *Ctenopterella* (Fig. 1: A1 & B1), *Dasygrammitis* (Fig. 1: A2 & B2), *Oreogrammitis* (Fig. 1: A3 & B3), *Prosaptia* (Fig. 1: A4 & B4) and *Themelium* (Fig. 1: A5 & B5);
2) In whorls, in *Calymmodon* (Fig. 3: A1 & B1), *Scleroglossum* (Fig. 3: A2 & B2; A3 & B3) and *Xiphopterella* (Fig. 3: A4 & B4); and
3) Spirally in *Acrosorus* (Fig. 2: A1 & B1), *Radiogrammitis* (Fig. 2: A2 & B2) and *Tomophyllum* (Fig. 2: A3 & B3).

   In the spiral arrangement, transverse sections of the rhizome show that the stipes were in fact arranged in a more-or-less "2+1" arrangement i.e. two stipes were at the same stage of development but there is another stipe in an another stage of development. This proved that the three stipes are not exactly a true whorl.

Table 1. Rhizome characteristics of Grammitidaceae taxa studied.

Species	Rhizome habit	Stipe arrangement	Vasculature
Acrosorus friderici-et-pauli	erect	spiral	solenostele
Acrosorus streptophyllus	erect	spiral	solenostele
Calymmodon curtus	erect	whorls	dictyostele
Ctenopterella blechnoides	creeping dorsiventral	horizontal rows	solenostele
Dasygrammitis brevivenosa	creeping dorsiventral	horizontal rows	solenostele
Dasygrammitis fuscata	creeping dorsiventral	horizontal rows	solenostele
Oreogrammitis adspersa	creeping dorsiventral	horizontal rows	solenostele
Oreogrammitis congener	creeping dorsiventral	horizontal rows	solenostele
Oreogrammitis malayensis	creeping dorsiventral	horizontal rows	solenostele
Oreogrammitis reinwardtii	creeping dorsiventral	horizontal rows	solenostele
Prosaptia alata	creeping dorsiventral	horizontal rows	solenostele
Prosaptia contigua	creeping dorsiventral	horizontal rows	solenostele
Prosaptia obliquata	creeping dorsiventral	horizontal rows	solenostele
Radiogrammitis holttumii	erect	spiral	solenostele
Radiogrammitis multifolia	erect	spiral	solenostele
Scleroglossum pusillum	erect	whorls	dictyostele
Scleroglossum sulcatum	erect	whorls	dictyostele
Themelium tenuisectum	creeping dorsiventral	horizontal rows	solenostele
Tomophyllum subminutum	erect	spiral	solenostele
Xiphopterella hieronymusii	erect	whorls	dictyostele
Xiphopterella sparsipilosa	erect	whorls	dictyostele

Two types of vasculature were identified, i.e., solenostele and dictyostele, similar to those results of Ogura (1972), Bishop (1988, 1989), Rakotondrainibe & Deroin (2006). Ogura (1972) also described the type of vasculature in the grammitids *Polypodium subpinnatifidum* (currently known as *Radiogrammitis subpinnatifida* (Blume) Parris) as solenosteles. The other type, the perforated dictyostele, occurs in *Ctenopteris sodiroi* (currently known as *Melpomene sodiroi* (Christ & Rosenst.) A.R.Sm. & R.C.Moran), *Grammitis* sp. and *Scleroglossum* sp. The results of the current study are similar to his study. The solenostele was found in *Acrosorus* (Fig. 2: B1), *Radiogrammitis* (Fig. 2: B2), *Tomophyllum* (Fig. 2: B3) (all with erect rhizomes and the stipes arranged spirally); and *Ctenopterella* (Fig. 1: B1), *Dasygrammitis* (Fig. 1: B2), *Oreogrammitis* (Fig. 1: B3), *Prosaptia* (Fig. 1: B4) and *Themelium* (Fig. 1: B5) (all with creeping dorsiventral rhizomes and the stipes arranged horizontally). The dictyostele occurs in *Calymmodon* (Fig. 3: B1), *Scleroglossum* (Fig. 3: B2 & B3) and *Xiphopterella* (Fig. 3: B4) (all with erect rhizomes and the stipes arranged in whorls).

Regarding the similarity in type of vasculature between genera, there are two probabilities. The first is that the similarities are possibly caused by the close

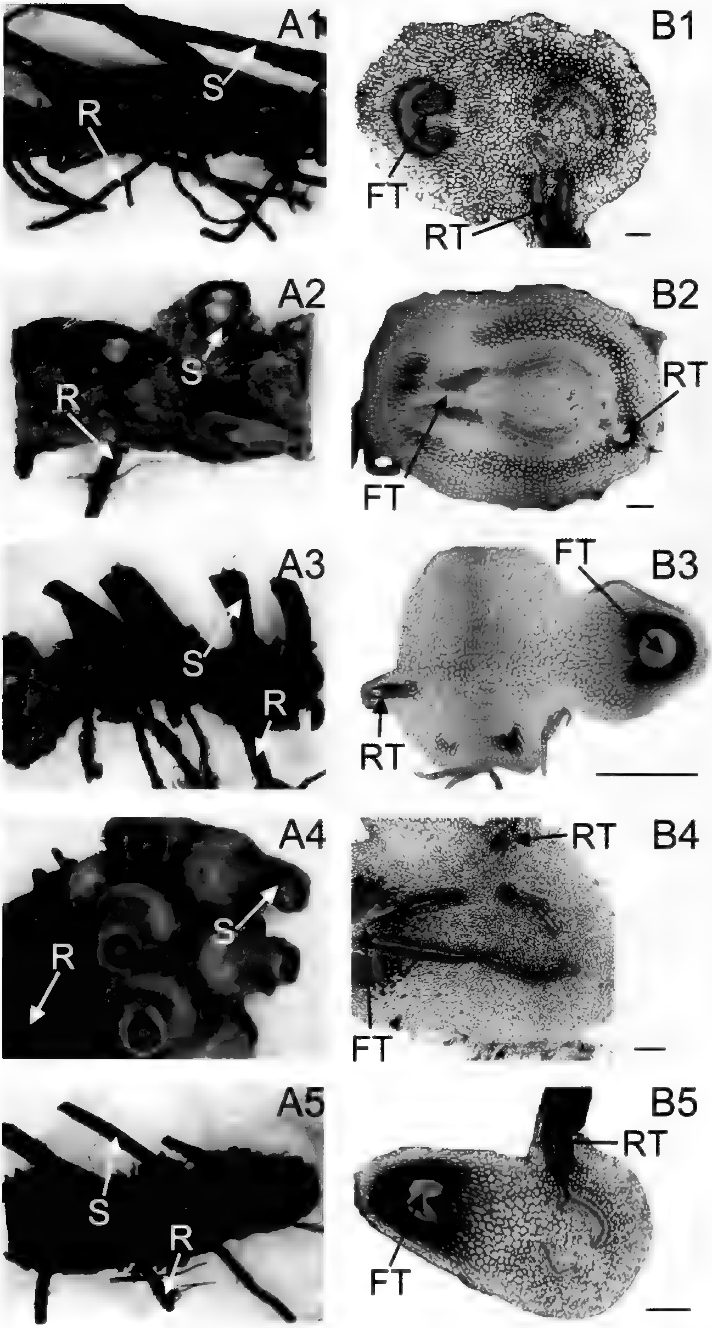

Fig. 1. Rhizome habit (A1–5) and anatomy (B1–5) in Grammitid species of the Solenostele group with creeping dorsiventral rhizomes and stipes arranged in horizontal rows. **A1 & B1.** *Ctenopterella blechnoides*; **A2 & B2.** *Dasygrammitis fuscata*; **A3 & B3.** *Oreogrammitis congener*; **A4 & B4.** *Prosaptia alata*; **A5 & B5.** *Themelium tenuisectum*. Bar equals 200 µm in B1, B2; 500 µm in B4 & B5 and 1000 µm in B3. Abbreviations used: S = stipe, R = root, FT = frond trace, RT = root trace.

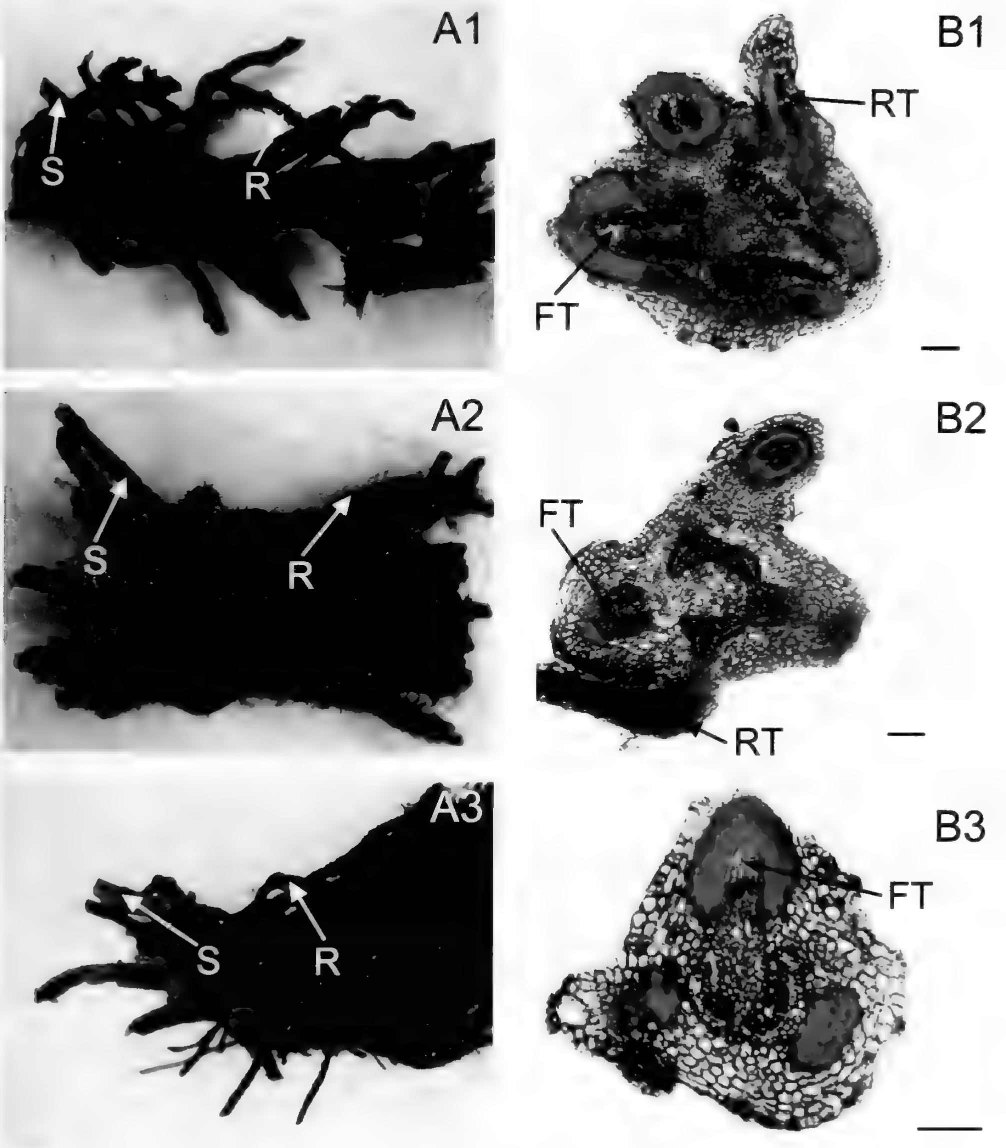

Fig. 2. Rhizome habit (A1–3) and anatomy (B1–3) in Grammitid species of the Solenostele group with erect rhizomes and stipes arranged spirally. **A1 & B1.** *Acrosorus friderici-et-pauli*; **A2 & B2.** *Radiogrammitis multifolia*; **A3 & B3.** *Tomophyllum subminutum*. Bar equals 200 μm in B1–B3. Abbreviations used: S = stipe, R = root, FT = frond trace, RT = root trace.

relationship between genera. For the solenostele group in the current study (*Acrosorus*, *Ctenopterella*, *Dasygrammitis*, *Oreogrammitis*, *Prosaptia*, *Radiogrammitis*, *Themelium* and *Tomophyllum*); the close resemblance between certain genera, e.g., (*Oreogrammitis* and *Radiogrammitis*; *Ctenopterella* and *Themelium*; *Dasygrammitis* and *Tomophyllum*) has been discussed by Parris (2007). The genera *Radiogrammitis*,

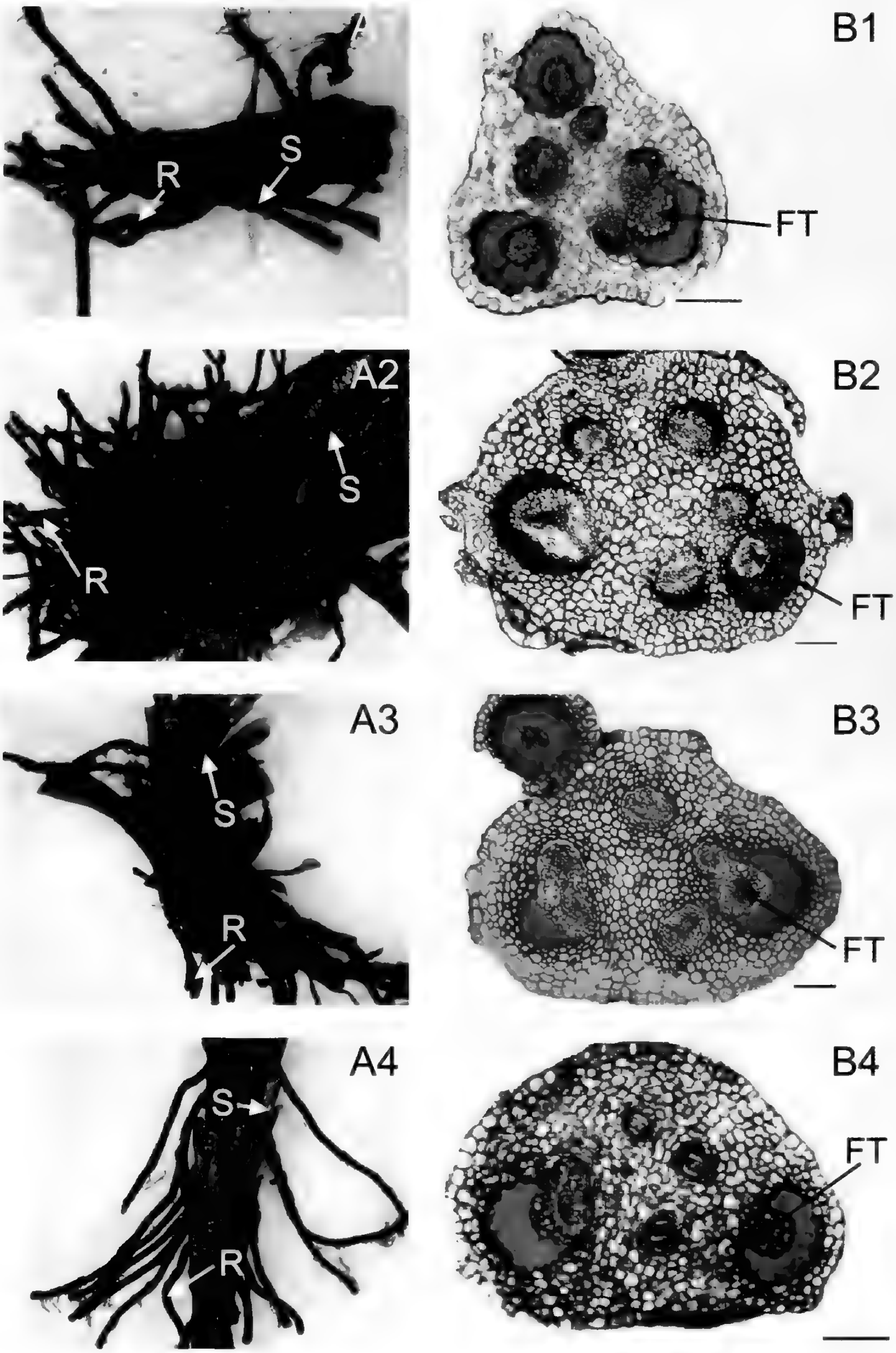

Fig. 3. Rhizome habit (A1–4) and anatomy (B1–4) in Grammitid species of the Dictyostele group with erect rhizomes and stipes arranged in whorls. **A1 & B1.** *Calymmodon curtus*; **A2 & B2.** *Scleroglossum pusillum*; **A3 & B3.** *Scleroglossum sulcatum*; **A4 & B4.** *Xiphopterella hieronymusii*. Bar equals 200 μm in B2–B4; 500 μm in B1. Abbreviations used: S = stipe, R = root, FT = frond trace.

Acrosorus and *Tomophyllum* share similarities in having solenosteles and stipes arranged spirally around the rhizome. However, on the basis of examining the close relationships between genera, the similarity of these characters does not agree with their placement in the phylogenetic tree in Ranker et al. (2004), where *Radiogrammitis* is placed near to *Oreogrammitis* and *Themelium* (due to its close resemblance to *Oreogrammitis* in many characters except its erect rhizome and the absence of rhizome scales in many species); while *Tomophyllum* falls within the same group with *Calymmodon* and *Scleroglossum*. However, not all the genera with solenosteles have been sampled for the cladistic analysis in Ranker et al. (2004). Four genera not yet included in the cladistic analysis are *Acrosorus*, *Ctenopterella*, *Dasygrammitis* and *Xiphopterella*. Hence, an explanation of the relationship between the genera in the solenostele group can only be proved once these four genera are included in the analysis. For the dictyostele group in the current study, the close relationship between *Calymmodon* and *Scleroglossum* was shown in the cladistic tree by Ranker et al. (2004), while the position of *Xiphopterella* in the same clade based on rhizome form and hair types, which was hypothesised in Parris (2007), agreed with the rhizome anatomy results.

The second probability is that the similarities might be due to a mechanical factor such as stipe arrangement on the rhizome. Ogura (1972) mentioned in general that the dictyostele occurs in species with overlapping leaf gaps. This is clearly seen with the occurrence of dictyosteles in genera with erect rhizomes and stipes arranged in whorls (*Calymmodon*, *Scleroglossum* and *Xiphopterella*); as well as the genera with creeping rhizomes and stipes arranged horizontally (*Ctenopterella*, *Dasygrammitis*, *Oreogrammitis*, *Prosaptia* and *Themelium*) that all have solenosteles. However, the occurrence of solenosteles in some species with erect rhizomes where the stipes are arranged spirally around the rhizome is not clearly understood. This is probably due to the non-overlapping of leaf gaps due to the spiral arrangement.

Ogura (1972) gave a brief description of the rhizome anatomy of the Polypodiaceae. The cortex and pith consist mostly of parenchyma. Sclerenchyma may occur in various forms and arrangements. In the current study, sclerenchyma around the vascular bundles was found in *Acrosorus friderici-et-pauli* (Christ.) Copel. (Fig. 4A), *Calymmodon curtus* Parris (Fig. 4B), *Scleroglossum pusillum* (Blume) Alderw. (Fig. 4C), *Xiphopterella hieronymusii* (C.Chr.) Parris (Fig. 4D) (all with erect rhizomes) and *Oreogrammitis malayensis* Parris (Fig. 4E) (with a creeping dorsiventral rhizome). One similarity between these plants is that almost all (except *Acrosorus friderici-et-pauli* and *Xiphopterella sparsipilosa*) are small-sized plants with the lamina length less than 10 cm. Hence, the sclerenchyma may function as supporting tissue in the plants.

Conclusions

Similarities in the type of vasculature among genera in the current study are seen as the result of the arrangement of stipes on the rhizome. It is consistent throughout the

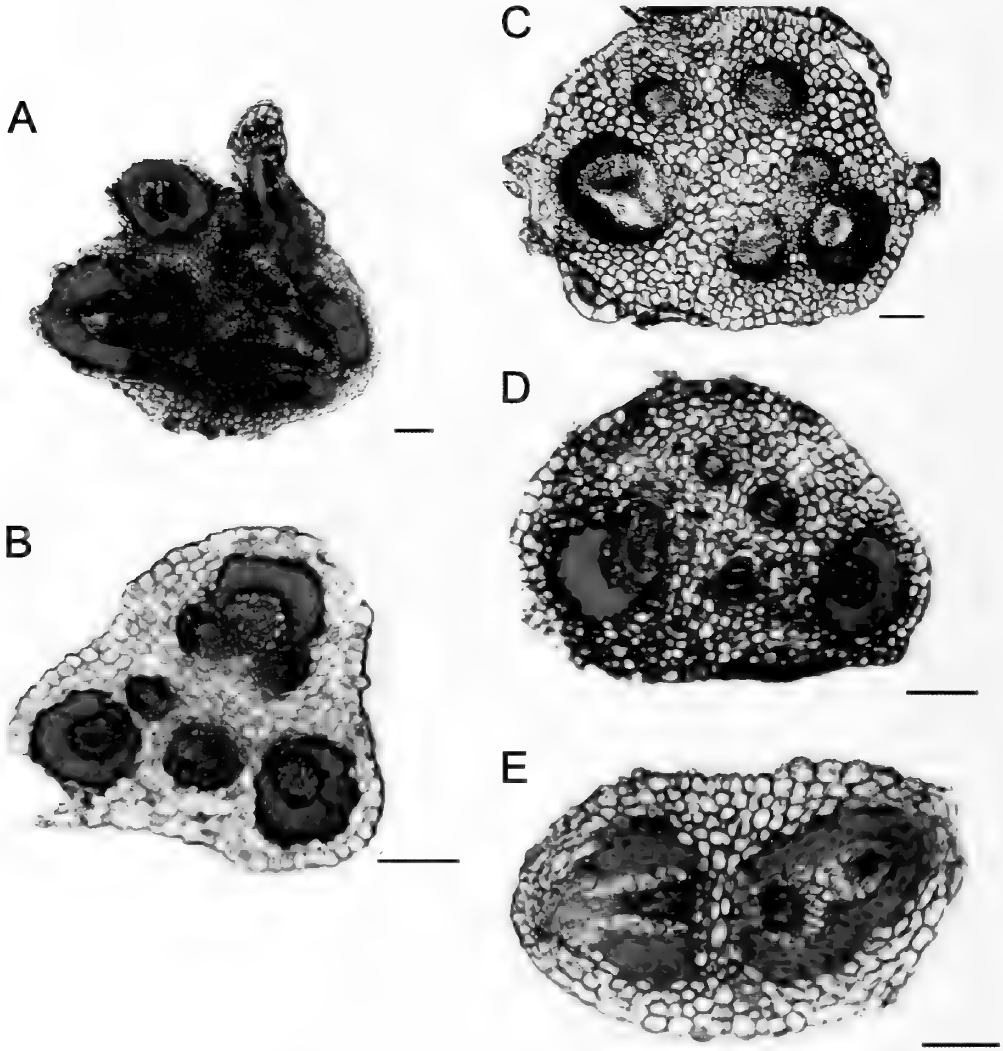

Fig. 4. Rhizome sections with red staining highlighting sclerenchyma tissue surrounding the vascular bundles. **A.** *Acrosorus friderici-et-pauli*; **B.** *Calymmodon curtus*; **C.** *Scleroglossum pusillum*; **D.** *Xiphopterella hieronymusii*; **E.** *Oreogrammitis malayensis*. Bar equals 200 µm in A, C–E; 500 µm in B.

study that overlapping of leaf gaps influences the formation of stele type. Whether the similarities are the result of close relationship among genera, it is only proven in certain cases, especially in the dictyostele group. For the solenostele group, a larger sampling is needed in the DNA analysis before such relationships can be assessed.

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Appendix A. List of specimens used for rhizome anatomy study. Bkt = Bukit (Malay for Hill), FR = Forest Reserve; G = Gunung (Malay for Mount)

Taxa	Specimens examined
Acrosorus friderici-et-pauli (Christ.) Copel.	*Nor Ezzawanis* FRI 52526, Cameron Highlands, G Brinchang, c. 1729 m asl, 17 Jan 2007 (KEP).
Acrosorus streptophyllus (Baker) Copel.	*Nor Ezzawanis* FRI 52395, Cameron Highlands, G Berembun, c. 1500 m asl, 19 Aug 2006 (KEP).
Calymmodon curtus Parris	*Nor Ezzawanis* FRI 52530, FRI 52531, Cameron Highlands, G Brinchang, c. 1729 m asl, 13 Jan 2007 (KEP).
Ctenopterella blechnoides (Grev.) Parris	*Nor Ezzawanis* FRI 54527, G Ledang, c. 1225 m asl, 15 Jan 2008 (KEP).
Dasygrammitis brevivenosa (Alderw.) Parris	*Nor Ezzawanis* FRI 52525, Cameron Highlands, G Brinchang, c. 1729 m asl, 13 Jan 2007 (KEP).
Dasygrammitis fuscata (Blume) Parris	*Nor Ezzawanis* FRI 52420, Cameron Highlands, G Berembun, c. 1500 m asl, 19 Aug 2006 (KEP), *Nor Ezzawanis* FRI 52521, FRI 52527, Cameron Highlands, G Brinchang, c. 1729 m asl, 13 Jan 2007 (KEP).

Oreogrammitis adspersa (Blume) Parris	*Nor Ezzawanis* FRI 54556, G Belumut, c. 1000 m asl, 22 to 24 Jan 2008 (KEP).
Oreogrammitis congener (Blume) Parris	*Nor Ezzawanis* FRI 52374, Cameron Highlands, G Brinchang, c. 1729 m asl, 18 Aug 2006 (KEP), *Nor Ezzawanis* FRI 52443, Cameron Highlands, G Berembun, c. 1500 m asl, 19 Aug 2006 (KEP).
Oreogrammitis malayensis Parris	*Nor Ezzawanis* FRI 54539, G Belumut, c. 1000 m asl, 22 Jan 2008 (KEP).
Oreogrammitis reinwardtii (Blume) Parris	*Nor Ezzawanis* FRI 52360, Cameron Highlands, G Brinchang, c. 1729 m asl, 18 Aug 2006 (KEP), *Nor Ezzawanis* FRI 52546, Cameron Highlands, G Brinchang, c. 1729 m asl, 14 Jan 2007 (KEP), *Nor Ezzawanis* FRI 52593, Genting Highlands, G Ulu Kali, c. 1767 m asl, 16 Feb 2007 (KEP).
Prosaptia alata (Blume) H. Christ.	*Nor Ezzawanis* FRI 54604, Berembun FR, Bkt Lantai, 9 Apr 2008 (KEP).
Prosaptia contigua (G. Forst.) C. Presl	*Nor Ezzawanis* FRI 52428, Bkt Larut FR, G Hijau, c. 1300 m asl, 20 Aug 2006 (KEP), *T.L. Yao* FRI 55924, Cameron Highlands, Parit Falls, 10 May 2007 (KEP).
Prosaptia obliquata (Blume) Mett.	*Nor Ezzawanis* FRI 52432, *FRI 52433*, Bkt Larut FR, G Hijau, c. 1300 m asl, 20 August 2006 (KEP), *Nor Ezzawanis* FRI 54460, Cameron Highlands, Ulu Telom, G Siku, c. 1486 m asl, 21 May 2007 (KEP).
Radiogrammitis holttumii (Copel.) Parris	*Nor Ezzawanis* FRI 54475, Cameron Highlands, Ulu Telom, G Siku, c. 1486 m asl, 21 May 2007 (KEP).
Radiogrammitis multifolia (Copel.) Parris	*Kueh H.L.* FRI 52544, Taman Negara, G Tahan, 3 to 4 Feb 2007 (KEP)
Scleroglossum pusillum (Blume) Alderw.	*Nor Ezzawanis* FRI 52592, Genting Highlands, G Ulu Kali, c. 1767 m asl, 16 Feb 2007 (KEP).
Scleroglossum sulcatum (Kuhn) Alderw.	*Nor Ezzawanis* FRI 52582, Genting Highlands, G Ulu Kali, c. 1767 m asl, 16 Feb 2007 (KEP).
Themelium tenuisectum (Blume) Parris	*Nor Ezzawanis* FRI 52591, Genting Highlands, G Ulu Kali, c. 1767 m asl, 16 Feb 2007 (KEP).
Tomophyllum subminutum (Alderw.) Parris	*Nor Ezzawanis* FRI 54482, Cameron Highlands, Ulu Telom, G Siku, c. 1486 m asl, 21 May 2007 (KEP).
Xiphopterella hieronymusii (C.Chr.) Parris	*Nor Ezzawanis* FRI 54464, Cameron Highlands, Ulu Telom, G Siku, c. 1486 m asl, 21 May 2007 (KEP).
Xiphopterella sparsipilosa (Holttum) Parris	*Kueh H.L.* FRI 52560, Taman Negara, G Tahan, 3 to 5 Feb 2007 (KEP)

Ethnomedicinal study of the Sundanese people at the Bodogol area, Gede Pangrango Mountain National Park, West Java

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ABSTRACT. Traditional medicine is often considered adequate even in present times, especially when modern medical treatment is diffficult to obtain. Indonesia, a country with rich biodiversity and a multicultural society, has a wealth of medicinal plant knowledge. Observations on the ethnomedicinal practices of the Sundanese people, conducted in several villages (Cipeucang, Ciwaluh, Lengkong Girang, Lengkong Hilir and Sungapan) around the Bodogol area in West Java, are summarised.

Keywords. Bodogol, ethnomedicine, Gede Pangrango Mountain National Park, Indonesia, medicinal plants, Sundanese people, West Java

Introduction

In traditional societies worldwide, plants feature importantly in the treatment of many ailments, in particular infectious and parasitic diseases, diarrhoea, fever and colds, as well as in birth control and dental hygiene. According to the World Health Organisation (WHO), traditional medicine is a rather vague term for distinguishing any ancient or culturally based health-care system from orthodox scientific medicine, or allopathy. This includes systems that are currently regarded as indigenous or unorthodox, alternative, folk, fringe, and even "unofficial". Both the major Asian systems (e.g., the Chinese, Ayurvedic, Unani, Unani Tibb medical systems), which are comparatively well documented since ancient times, as well as the less widespread, largely orally transmitted practices of other traditional communities, are included in this understanding of traditional medicine. It is estimated (Farnsworth 1994, Cotton 1996) that about 64% of the world's population depends on some form of traditional medicine for their health care needs.

It was not until the 1970's that a more organised study of traditional medicine and herbal remedies received due academic attention. The World Health Organisation, seeing the success of Chinese heterox healthcare programmes, began to encourage studies and approaches that aimed at combining traditional and Western resources. Effective ethnomedicinal research should consider related aspects, such as traditional concepts of the origins of disease and local perceptions of the efficacy of particular treatments, applicable even when there is detailed documentation already available, and certainly for orally transmitted practices. The study of ethnomedicine in a cultural context is largely medical ethnobotany, involving the identification of botanical species used in traditional remedies and even understanding folk classification of medicinal plants (Balick & Cox 1996). Frequently, ethnobotanical inventories of plant species used in healing are drawn up from interviews or surveys based on collection of voucher specimens in a given area (Jain & Mudgal 1999). Some studies are based on the identification of medicinal plants sold in markets.

Treatments with Old World medicinal plants were mentioned in the *Materia Medica* of Dioscorides in the first century BCE. As scientists of western civilisations became more interested in medicinal plants from Asia, Jacobus Bontius who worked for the VOC (East India Company) conducted research on Javanese medicinal plants in the 1600s, and the German naturalist Rumphius, who became deeply involved in the study of plants and animals in Indonesia in the 1700s, also documented plants known as cures. In the 1800s, during the British occupation, Thomas Horsfield assisted Raffles in studying medicinal plants of Central and East Java. Their work inspired others, who became engaged in ethnobotany (see Klokke 1998).

In fact, the study of medicinal plants should be emphasised for Indonesia, which has a rich biodiversity and a multicultural society with long-standing knowledge in the different forms of ethnomedicine and plant use. We carried out research into the knowledge of medicinal plants in several villages around the villages of Bodogol, viz., Lengkong Girang, Ciwaluh, Cipeucang, Lengkong Hilir, and Sungapan. The study was conducted from November 18th to 22th 2008.

Study site and overview of the Sundanese people

West Java occupies a total area of 35,746.026 square kilometres, consisting of 16 counties and 9 cities. West Java is known for its fertility and there is still an active volcano. The region ranges generally from flat to undulating, to hilly and mountainous in parts. Annual rainfall exceeds 2000 mm. The villages in the Bogor regency where research was conducted include Sungapan village, Lengkong Hilir, Ciwaluh, Lengkong Girang (a part of Wates Jaya village), and Cipeucang (including rural areas in Buncir Sand). These villages engage much in rice cultivation, but medicinal plants can still be found in the wild or are planted.

As a tribe, the Sundanese were forerunners of civilisation established in the Indonesian archipelago, beginning with the founding of Salakanagara, the oldest kingdom in Indonesia. Descendants of this Sunda Kingdom have founded other great kingdoms in the archipelago, including Sriwijaya, Majapahit, Mataram Kingdom, the Kingdom of Cirebon, and the Kingdom of Banten. Sunda is the culture of the people who live in West Java. The Sundanese believe that they should possess the ethos or character for a virtuous life in their culture, often described as *Kasundaan* ("Sundanese-ness"). Many Sundanese expressions representing good, white, clean, or bright exist; and the moral characteristics of *cageur* (Sundanese for 'healthy'), *bageur* (good), *bener* (right), *singer* (introspective), and *pinter* (intelligent) have existed for over a thousand years.

Sundanese people traditionally eat various kinds of plants and seeds obtained from their gardens or fields. Commonly available plants that are sometimes used for healing are called *lalap*.

Methods

Medicinal plant species were collected in five villages around Bodogol, and for 80% of these, uses were documented through surveys and interviews (Table 1). Sometimes, different local names for the same medicinal plant species were available from different persons, and different tribes; this was also checked through further interaction with the local shaman (*paraji*). The results obtained include those from the interview and persons who have expertise in treatment, as well as elderly individuals who are considered knowledgeable about medicinal plants. In recording the plant names and uses, herbarium specimens were also taken for identification and as vouchers. Notes on plant use also included the plant parts that were taken. A local resident served as translator during interviews. Informants were asked to describe their knowledge about traditional medicine; how medicinal plants were prepared for particular treatments; how their knowledge was acquired; and how they disseminated their skills. The literature was also consulted where possible.

Results and discussion

Perception about illnesses

Based on the interviews, the Sundanese perception is that disease can be caused by behaviours which lead to imbalance in the body elements, in addition to diseases caused by the supernatural, such as spirits. Imbalance in the body can be due to poorly balanced diet or excessive and uncontrolled human emotion such as fear, hate or joy.

Members of the community who were interviewed accept that a person is truly ill and in pain only when he is suffering from chronic disease or other health problems that cause work activities to be disrupted. Even if a person has minor problems such as colds, he is not considered ill if his work routine is not disrupted.

Plants in traditional medicine

The theory of disease (Foster & Anderson 1978) includes belief in natural health, causes of disease and different types of medicine and healing techniques. In the traditional theory of disease, pain is usually accepted as a consequence of some taboo being broken, or an imbalance between hot and cold elements in the body. Local knowledge is that which is traditionally owned and developed by a community in response to, and in interaction with, its environment. According to Koentjaraningrat (1989), each culture has a complex set of knowledge about nature, and the plants, animals, objects and people around them that are abstracted into the concept, theory, and establishment (*koentjaraningrat*). Traditional healers, in this case a shaman, *datu*, or teacher, provide explanations and interpretations about the illness and the use of materials or herbs for treating or curing diseases.

In this paper, the results represent part of the local knowledge of medicinal plants of the Sundanese people in five villages around Bodogol. Basically, people in all villages visited are still very dependent on the plants around them. In addition to medicine, they also use it as animal feed for such as goats and sheep, for firewood, and also to make household appliances. Among the five villages visited, three essential aspects of traditional treatment using medicinal plants were noted. First was the prominence of treatment after, or the recovery from, childbirth, which is usually done by the *paraji*. Second was the existence of persons who believed that they had the ability to cure diseases. Third was that treatment typically made use of plants around the community, which can be easily obtained.

Treatment techniques are varied. There are plants that can be eaten as part of the treatment. Sometimes, plant parts are brewed with hot water, grated and kneaded and then applied onto an affected body part to be treated. Another use is by mixing with other ingredients and then boiling to obtain a concoction or infusion that is taken orally. A fourth way is to incorporate a medicinal herb into food dishes, for example, by frying in mixture with egg. One other way is by soaking the plant material and bathing with the infusion. Knowledge of such treatment methods is obtained from parents and the community at large.

The 80 medicinal plants recorded around the five villages are listed in Appendix A. An important use of medicinal plants is for recovery after childbirth. Often, a woman who has just given birth will make a *godogan* consisting of roots and leaves of *buntiris* (*Kalanchoe pinnata* Pers., Crassulaceae), *babadotan* (*Ageratum conyzoides* L.), *daun rane* (*Sellaginela plana* (Desv.) Hieron.) and *jawer kotok* (*Plectranthus scutellarioides* (L.) R.Br.). Plants that are often mentioned by informants include *buntiris* and *kumis kucing* (*Ortosiphon aristatus* (Blume) Miq., Lamiaceae). Being easy to obtain, *buntiris* is still often used to treat fever in children, while *kumis kucing* is believed to cure various diseases. In these five villages, most community gardens are planted with *kumis kucing*, which is sold to cities.

For 46 medicinal plant species recorded in Lengkong Girang Village, the uses were for curing or treating fever (15 species), sprue (1 species), pain in the digestive tract (3 types), high blood pressure (2 types), decreased vitality (8 types), skin diseases (3 types), stroke (3 kind), injuries due to knives (1 species), toothache (1 species), recovery after childbirth (5 types), and *ambayen* (1 species). These mainly utilised leaves (37 species), roots (3 types), seeds (1 species), and tubers (4 types).

In Ciwaluh Village, 23 species of medicinal plants were recorded, used for treating fevers (3 types), recovery after childbirth (8 types), diarrhea (1 species), knife wounds (1 species), nausea and convulsions (1 species), pain when defecating and urinating (2 types), hypertension (1 type), and as an "energy booster" (2 types) and general medicine for all diseases (1 species). The plant parts used were leaves (17 species), roots (1 species), bulbs (2 types), and stems (2 species).

At Cipeucang Village, 29 species of medicinal plants were documented, for treating bone fractures (4 types), diabetes (1 type), kidney problems (2 types), cancer (2 types), low vitality (2 types), fevers (2 species), recovery after childbirth (7 species), coughs (2 types), abdominal pain (2 types), constipation (1 types), skin diseases (1 species), knife wounds (2 types); also generally for all diseases (3 types), and for casting out spirits from young children (1 species). The parts used were leaves and flowers.

From Lengkong Hilir Village, 16 species of medicinal plants were recorded. These were for curing fevers (3 types), pain in the digestive tract (4 types), hypertension (2 types), sprue (1 type), heatiness (1 species), low vitality (5 types), skin diseases (1 type), back pain (4 types), fatigue (3 types), and toothache (1 species).

At Sungapan Village, 17 species of medicinal plants were recorded, used for treating fevers (1 species), pain in the digestive tract (2 types), gout (4 types), diabetes (4 type), low vitality (4 species), recovery after childbirth (1 species), bleeding after childbirth (3 types), dizziness (1 species), cough (1 species), anaemia in women (1 species), and sore eyes (1 species). All these utilised only leaves.

At the present time with more advanced medical facilities and many kinds of medicines commercially available shops, drugstores and pharmacies, it is possible that there should be increasing erosion of medicinal plant knowledge. However, in many cases, people still remember traditional herbal treatments they were taught by their parents. The interviews verified that old people knew more about what plants are used as medicines than younger people, and clearly parents who used medicinal plants attempted to pass this knowledge down to their children. According to Ms. Pupu, a resident of Ciwaluh Village, if someone had knowledge that is not utilised, they will not be rewarded after death.

The people who still use medicinal plants do not strongly believe in modern drugs. It is also for economic reasons that they use medicinal plants, which are cheaper and easier to obtain. Conversely, those who have switched over to modern medicine say that modern medicine heals faster and was more convenient because it does not require any processing by the user beforehand. Medicinal plants are usually the "first aid" or a "last resort". This can be gathered from the interviews with Ms. Yanti in Cipeucang Village, who suffered from chronic cough. She visited the doctor but the cough did not go away, and eventually tried *capituheur* (*Mikania cordata* (Burm.f.) B.L.Rob.), a plant believed to cure coughs. After drinking an infusion regularly, the coughing ceased. In contrast, Mr. Ujang, a resident of Lengkong Hilir Village, took *hantap* (*Sterculia rubiginosa* Vent.) as a kind of "first aid" for a toothache.

Conclusion

Knowledge of medicinal plants in the five villages studied appears to be still substantial, but perhaps just changing. It can be sensed, however, that when there is reduced dependency on medicinal plants, knowledge of plant uses will become increasingly reduced. Culture is dynamic and growing, and more changes will definitely come (Naranjo 1997). There is certainly an urgent need to document this knowledge.

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Appendix A. List of 80 medicinal plant species recorded in the Bodogol area, West Java. The villages studied are Cipecang (CP), Ciwaluh (CW), Lengkong Girang (LG), Lengkong Hilir (LH) and Sungapan (S). A '+' indicates that the species was recorded at a particular village.

Local Name	Species, Family	CP	CW	LG	LH	S
Akar eurih	*Imperata cylindrica*, Poaceae	+		+	+	
Alpukat	*Persea americana*, Lauraceae	+			+	
Antanan	*Centella aciatica*, Apiaceae		+	+		+
Babadotan	*Ageratum conyzoides*, Asteraceae	+	+	+		+
Babawangan	*Peperomia pelucida*, Piperaceae			+	+	
Baluntas	*Clerodendrum buchananii*, Lamiaceae			+		
Bawang merah	*Allium cepa*, Amaryllidaceae		+	+		+
Bawang putih	*Allium sativum*, Amaryllidaceae			+		
Bijangut	*Mentha arvensis*, Lamiaceae	+				
Brotowali	*Tinospora crispa*, Menispermaceae	+				
Buntiris	*Kalanchoe pinnata*, Crassulaceae		+	+		+
Capituheur	*Mikania cordata*, Asteraceae	+				
Cecenet	*Physalis minima*, Solanaceae	+		+	+	
Cengkeh	*Syzygium aromaticum*, Myrtaceae			+		
Daun calincing	*Oxalis corniculata*, Oxalidaceae			+		
Daun cengek	*Capsicum frutescens*, Solanaceae					+
Daun jambu	*Psidium guajava*, Myrtaceae		+	+		+
Daun kapuk	*Ceiba pentandra*, Malvaceae			+		

Daun katomas	*Euphorbia heterophylla*, Euphorbiaceae	+				
Daun kopi	*Coffea arabica*, Rubiaceae	+				
Daun mangga	*Mangifera indica*, Anacardiaceae	+				
Daun paria	*Momordica charantia*, Cucurbitaceae			+	+	
Daun penurun tensi darah tinggi	*Pilea microphylla*, Urticaceae				+	
Daun putri malu	*Mimosa pudica*, Leguminosae			+		
Daun rambutan	*Nephelium lappaceum*, Sapindaceae	+				
Daun rane	*Sellaginela plana*, Sellaginellaceae	+	+	+		+
Daun saga	*Abrus precatorius*, Leguminosae	+				
Daun sembung	*Blumea balsamifera*, Asteraceae			+		
Daun seureuh	*Cymbopogon citratus*, Poaceae			+		
Daun sirih	*Piper betle*, Piperaceae	+				
Daun sirsak	*Annona muricata*, Annonaceae	+		+		
Daun waru	*Hibiscus tiliaceus*, Malvaceae	+				
Daun wera hijau dan merah	*Hibiscus rosa-sinensis*, Malvaceae			+		
Gedang ganul	*Carica papaya*, Caricaceae			+		
Gedebong	*Piper umbellatum*, Piperaceae		+			
Hantap	*Sterculia rubiginosa*, Sterculiaceae	+			+	
Jambe/pinang	*Arecha catechu*, Arecaceae	+				
Jawer kotok	*Plectranthus scutellarioides*, Lamiaceae	+	+	+		+
Jotang	*Spilanthes iabadicensis*, Asteraceae	+				
Kaca piring	*Gardenia jasminoides*, Rubiaceae		+	+		+
Kahitutan	*Lasianthus inodorus*, Rubiaceae				+	
Karas tulang	*Turpinia montana*, Staphyleaceae		+			+
Katomas	*Euphorbia heterophylla*, Euphorbiaceae				+	
Kaworo	*Abelmoschus moschatus*, Malvaceae		+			+
Kecubung merah dan putih	*Datura metel*, Solanaceae			+		
Keluwih	*Artocarpus camansi*, Moraceae			+		
Ki beling	*Sericocalyx crispus*, Acanthaceae				+	
Ki koneng	*Arcangelicia flava*, Menispermaceae	+		+		
Ki korejat	*Laurentia longiflora*, Campanulaceae			+		
Ki rapet	*Ficus villosa*, Moraceae		+			+
Ki saat	*Artemisia vulgaris*, Asteraceae					+
Ki senok	*Abelmoschus manihot*, Malvaceae				+	
Ki tajam	*Clinacanthus nutans*, Acanthaceae	+		+		
Ki urat	*Plantago major*, Plantaginaceae		+	+		+
Kirinyuh pait	*Eupatorium inulifolium*, Asteraceae	+				
Kumis kucing	*Ortosiphon aristatus*, Lamiaceae	+	+	+	+	+
Kunci	*Boesenbergia rotunda*, Zingiberaceae		+	+		+

Kunyit	*Curcuma longa,* Zingiberaceae			+		
Lampuyung	*Symphytum officinale,* Boraginaceae	+	+			+
Lempuyang	*Zingiber aromaticum,* Zingiberaceae				+	
Lengkuas	*Alpinia galanga,* Zingiberaceae			+		
Monyenyen	*Laurentia longiflora,* Campanulaceae			+		
nanangkaan	*Euphorbia hirta,* Euphorbiaceae				+	
Panglay	*Zingiber ottensii,* Zingiberaceae	+		+		
Pecah beling	*Strobilanthes crispus,* Acanthaceae	+		+		
Pungpulutan	*Urena lobata,* Malvaceae			+		
Putat	*Planchonia valida,* Lecythidaceae			+		
Rasamala	*Altingia excelsa,* Hamamelidaceae			+		
Remek daging	*Excoecaria cochinchinensis,* Euphorbiaceae	+		+		
Rendeu	*Staurogyne elongata,* Acanthaceae		+			+
Sambiloto	*Andrographis paniculata,* Acanthaceae			+		
Sanagori	*Sida rhobifolia,* Malvaceae		+	+		+
Sawi langit	*Vernonia cinerea,* Asteraceae				+	
Seureuh	*Cymbopogon citratus,* Poaceae	+	+			+
Sintrong	*Erechites valerianifolia,* Asteraceae			+	+	
Tapakliman	*Pseudoelephanthopus spicatus,* Asteraceae			+		
Tawulu	*Premna obongata,* Lamiaceae		+			+
Terong kori	*Solanum aculeatissimum,* Solanaceae			+		
Walang	*Wedelia biflora,* Asteraceae	+	+	+		+

Instructions for contributing authors (*continued*)

Title and authorship. The title should concisely describe the contents. If a scientific name is used, its authority is normally excluded, but the family name would be provided. Authors' names, affiliations and postal / e-mail addresses are stated below the title. If more than one author, indicate "corresponding author". Avoid footnotes. A short **running title** (up to six words) should also be provided.

Abstract. The abstract is at most 100–300 words. It should concisely indicate the article's contents without summarising it; mentioning novelties and name changes. ***Keywords:*** Suggest at most eight keywords, in alphabetical order.

Scientific names and author abbreviations. Genus and species names of organisms must be italicised and followed by the authority (with family name in parentheses) when first mentioned in the text or diagnoses. Standards for author abbreviations include:

Brummitt, R.K. & Powell, C.E. (1992) *Authors of Plant Names*. Kew: Royal Botanic Gardens, Kew.

Kirk, P.M. & Ansell, A.E. (1992) *Authors of Fungal Names* [Index to Fungi Supplement]. Wallingford: CAB International.

Herbarium abbreviations (http://sciweb.nybg.org/science2/IndexHerbariorum.asp) follow

Holmgren, P.K., Holmgren, N.H. & Barnett, L.C. (eds) (1990) *Index Herbariorum. Part I: The Herbaria of the World* [Regnum Veg. vol. 120]. New York: New York Botanical Garden.

Journal and book title abbreviations. For journals:

Bridson, G.D.R., Townsend, S.T., Polen, E.A. & Smith, E.R. (eds) (2004) *BPH-2: periodicals with botanical content: comprising a second edition of Botanico-Periodicum-Huntianum.* Pittsburg: Hunt Institute for Botanical Documentation.

For books:

Stafleu, F.A. & Cowan, R.S. (eds) (1976–88) *Taxonomic Literature.* 2nd edition. 7 vols [Regnum Veg. vols 94, 98, 105, 110, 112, 115, 116].

Stafleu, F.A. & Mennega, E.A. (eds) (1992–) *Taxonomic Literature.* Supplements [Regnum Veg. vols 125, 130, 132].

(A useful source of verifying names of publications is
<http://asaweb.huh.harvard.edu:8080/databases/publication_index.html>. If in doubt, list full titles.

Other abbreviations and units of measurement. If using standard abbreviations and acronyms, give the full term on first mention. Dates are cited as: 1 Jan 2000. SI (metric) units of measurement are used and spelled out except when preceded by a numeral; they are abbreviated in standard form: g, ml, km, etc.

Tables. Tables are numbered in arabic numerals in the order they are first mentioned in the text and carry an indicative legend at the head. Tables are given at the end of the manuscript.

Illustrations. All drawings, maps, graphs and photographic images (individually or collected in a plate) are to be numbered in arabic numerals in the order they are first mentioned in the text, as Fig. 1, Fig. 2, etc. (plate components would be referred to in the text as Fig. 1A, 1B, Fig. 1A–D, etc.). If relevant, scale bars should be used to indicate magnification.

When grouping photographs, the maximum page area 19.5 × 13 cm must be heeded. High resolution digital images may be submitted as *separate* files (line drawings in black and white at 600 dpi, photographs at 300 dpi) sent electronically or in a CD. Do not embed images into the main text file.

References in the text. Citation in the text should take the form: King & Gamble (1886) or (King & Gamble 1886), or King et al. (1886) if more than three authors to a work. Use 2000a, 2000b, etc. if several papers by the same author(s) in one year are cited.

References listed at the end. There, works mentioned in the text are listed alphabetically as follows:

Dallwitz, M.J., Paine, T.A. & Zurcher, E.J. (1999) User's Guide to the DELTA Editor. http://biodiversity.uno.edu/delta/ (accessed on 2 Aug. 2010).

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References to web-based resources should include either a doi (digital object identifier) specification or full URL mentioning also the date it was accessed. Use of DNA sequences from GenBank should be acknowledged and the studies for which the sequences were generated should be cited.

Style of nomenclatural summaries. The following style is required:

Gardenia anisophylla Jack ex Roxb., Fl. Ind. ed. Carey & Wall. 2: 561 (1824).

Medinilla alternifolia Blume, Mus. Bot. 1: 19 (1849).

If authors include full bibliographic data for these works in the list of references at the end of the paper, they should also be mentioned in the text briefly, e.g., "Nomenclatural references researched include Blume (1849) and Roxburgh (1824)."

Homotypic synonyms should be provided in a block, stating the type at the end.

Front cover picture: *Shorea albida* canopy, Brunei Darussalam (Photo by K.M. Wong)
Back cover picture: *Kopsia singapurensis*, Singapore (Photo by Y.W. Low)

Flora Malesiana

was founded by Professor C.G.G.J. van Steenis (1901–1986)
who was enthralled by the vegetation and flora of the Malay Archipelago
and sought the most logical platform for an organised documentation
of the fascinating and valuable plant life of this region.
The Flora Malesiana Symposium was first held in Leiden
in 1989 to commemorate this eminent scholar, and is held once
every three years. The 8th Symposium was hosted by the
Singapore Botanic Gardens on 23–27 August, 2010.

From its initial objective, to obtain taxonomic documentation of the enormous botanical heritage of Malesia (the distinct botanical region recognised by van Steenis, including the Malay Peninsula, Sumatra, Java, the Lesser Sundas, Borneo, the Philippines, Sulawesi, the Moluccas, New Guinea and smaller associated islands), the Flora Malesiana has come to represent an umbrella project that includes not only revisions and flora writing. It now motivates and receives contributions from all kinds of taxonomic and systematic work, involving identification, inventories and other biodiversity assessments, checklists, and other biological studies on plants and their interactions. It is a huge flora and a vast endeavour, one which has attracted the interest of many countries, especially those in the flora area (Brunei, Indonesia, Malaysia, Papua New Guinea, Philippines, Singapore, Thailand), and neighbouring territories spanning the Indo-Burmese, East Asian and Indo-Chinese regions across to the Southwest Pacific and Australian regions, as well as institutions and individuals worldwide who wish to participate in discovering and documenting one of the richest floras on Earth.

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